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Editor:
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Fisheries Research Board of Canada
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Body Fluid Regulation in Smolting Atlantic Salmon[1,2]

By Arthur H. Houston[3] and Lawrence T. Threadgold[4]

ABSTRACT

Parr–smolt metamorphosis in yearling Atlantic salmon was accompanied by variations in plasma and tissue electrolyte levels, and in tissue water distribution. Plasma chloride declined sharply with the onset of smoltification, but recovered to values somewhat higher than those seen in parr with the attainment of the silvery parr stage. Some decrease, with no evidence of a secondary increase, was observed in tissue chloride concentrations. Changes in chloride space values suggested that parr–smolt metamorphosis is also characterized by a shift of tissue fluids from the extracellular to the cellular phase. These variations in water–electrolyte balance are thought to reflect a premigratory activation and secondary suppression of the extrarenal salt excretion systems employed for osmotic and ionic regulation in sea water. Their occurrence in fish estimated upon the basis of morphological characters to be large parr suggests that the metamorphic process may occur earlier in the life cycle of this species than is generally recognized.

INTRODUCTION

Smoltification of migratory salmonids is associated with marked changes in morphology, chemical composition, physiological and biochemical function, and behaviour (Hoar, 1953, 1958; Fontaine, 1954). The need of these animals for regulatory mechanisms capable of meeting relatively abrupt increases in environmental salinity suggests, however, that variations in water–electrolyte metabolism and its control are of pre-eminent importance. It is unlikely that the osmoregulatory systems employed by freshwater-adapted juvenile salmon are greatly different from those used by non-migratory teleosts (Black, 1957). Premigrant salmonids presumably meet their basic problems, osmotic overhydration and salt loss, through the production of a voluminous dilute urine, and by the dietary uptake or active absorption of inorganic ions. Such adaptations are obviously entirely unsuitable for life in a medium where osmotic dehydration and salt-loading are the central problems. Nevertheless, it has been abundantly demonstrated that following smoltification these species can tolerate the internal changes which accompany entry into sea water, and will within relatively short periods of time restore body fluid conditions to levels near those of the freshwater-adapted animals. (Gordon, 1959a, b; Houston, 1959a, b, 1960, 1961; Parry, 1961).

The rapidity with which the conversion from hyperosmoregulation to hypoosmoregulation takes place suggests that a premigratory modification of

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[2]Contribution from the Departments of Anatomy and Biology, Dalhousie University, Halifax, with the financial assistance of the National Research Council of Canada.
[3]Present address: Fisheries Laboratory, Department of Zoology, University of Manitoba, Winnipeg.
[4]Present address: Department of Zoology, The Queen's University, Belfast.

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water–electrolyte metabolism occurs, a suggestion supported by several observations that ionic and osmotic regulation is impaired during the later stages of freshwater life (Fontaine, 1951; Houston, 1959b, 1960; Koch *et al.*, 1959). However, data pertinent to this question are scanty, relatively little being known of osmotic and ionic regulation in smolting salmon. The present investigation was undertaken to provide further information regarding the regulatory abilities of juvenile salmon during this process. Particular emphasis has been placed in this investigation upon the distribution of water between the extracellular and cellular phases of muscle as a criterion of osmotic regulation. Since biological membranes are, on the whole, freely permeable to water, transient or continuing inequalities in the solute concentrations of cellular and extracellular fluids must inevitably lead to osmotic shifts of water tending to restore concentration equilibrium (Robinson, 1960). Because of this, tissue fluid distribution should provide a more reliable indication of overall osmoregulatory ability than the more commonly determined freezing point depression of the plasma, or the concentration of any single species of blood or tissue electrolyte, although the latter are useful as criteria of ionic regulation.

MATERIALS AND METHODS

Origin and Maintenance of Fish Stocks

Stocks of yearling Atlantic salmon used in this investigation were obtained from the Department of Fisheries of Canada Fish Culture Stations at Grand Lake and Coldbrook, Nova Scotia, through the courtesy of Mr J. M. Butler. The animals were transported to the University as required and maintained in dechlorinated Halifax city water in spray-aerated, fiber glass-lined, recirculating aquaria at 11.0±0.2° C. The aquaria were lighted for 8–10 hr each day, and the fish starved prior to use. Except in one instance few deaths occurred during transport, and the "delayed mortality" commonly associated with the movement of salmonids was slight. The animals were dipped on three successive days after arrival at the University in 0.1% tetracycline, and thereafter small amounts of this antibiotic were added to the aquaria weekly. The fish displayed no obvious symptoms of disease, and remained in active and apparently healthy condition throughout holding and experimental periods.

Sampling

Individual salmon were narcotized for 5–10 min prior to sampling in aqueous tricainemethane sulphonate (MS.222, 1:10,000). Narcotized animals were mounted ventral side uppermost upon a frame and the heart exposed. Blood was drawn directly from the conus arteriosus by light mouth suction through waxed 24 gauge needles into polyethylene catheter tubing lightly dusted with dry sodium heparin. Samples were immediately centrifuged, and the plasma decanted off and frozen in polyethylene containers prior to analysis.

Muscle tissue samples were excised from the dorsal fin area of both epaxial muscle bands, rapidly dissected free of obvious fat, bone, connective tissue and scales, wrapped in Parafilm, and frozen until required for analytical preparation.

The weight and fork length of each animal was recorded, and its stage of development estimated upon the basis of criteria similar to those employed by Evropeitseva (1957):

Parr: no apparent silvering, body colour greenish-yellow, belly dark, parr marks dark and clearly delineated;

Silvery parr: moderate degree of silvering, parr marks light in colour and more or less peripherally indistinct;

Smolt: moderate to heavy silvering, belly light in colour, parr marks absent or just visible under oblique light, body more slender than that of parr.

Coefficients of condition were calculated as 100 × weight in grams/fork length in centimetres.

Analytical Procedures

Plasma chloride determinations were made on 50-μl samples by a modification of the Schales and Schales (1941) procedure in which nitric-citrate buffer was substituted for distilled water as the sample dilutant. Muscle chloride was estimated by the modified "open Carius" procedure of J. F. Manery (1955, personal communication) as described in earlier studies (Houston, 1959a).

The volume of the extracellular phase was estimated by the chloride space technique, using the simplified procedure of Conway (1957).

$$(1) \quad \ldots\ldots \quad H_2O^{\text{ecs}}_{Cl^-} = \frac{({}_t{}^{Cl^-})}{({}_p{}^{Cl^-})} (0.9)\,(1000)$$

where: $H_2O^{\text{ecs}}_{Cl^-}$ = chloride space

${}_t{}^{Cl^-}$ = tissue chloride concentration, mM/kg

${}_p{}^{Cl^-}$ = plasma chloride concentration, mM/l.

The volume of the cellular phase was estimated as the difference between chloride space and tissue water content.

$$(2) \quad \ldots\ldots \quad H_2O^{\text{ics}}_{Cl^-} = {}_tH_2O - H_2O^{\text{ecs}}_{Cl^-}$$

where: $H_2O^{\text{ics}}_{Cl^-}$ = cellular space

${}_tH_2O$ = tissue water content, g/kg.

RESULTS

Weight–Length Retationship during Parr–Smolt Metamorphosis

Observations on changes in weight–length relationship during parr–smolt transformation are based upon values for 90 fish (Fig. 1), the animals being separated into three developmental stages as previously described.

Weight alone did not provide a reliable criterion for developmental stage as can be seen fron the overlap of parr and silvery parr, and silvery parr and smolt. Parr and smolt, however, were clearly separated.

An inflection in the weight–length relationship, suggestive of a major variation in growth pattern was apparent. Trend lines visually fitted through the

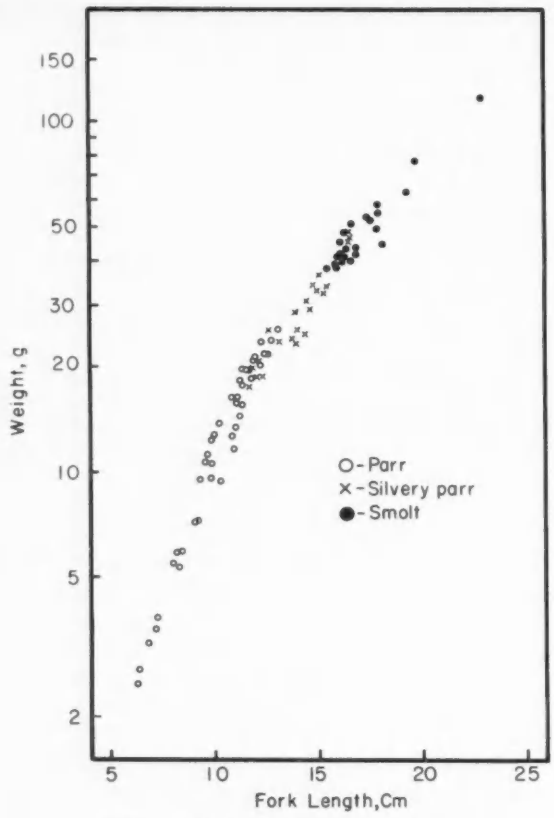

FIG. 1. Weight–length relationship.

two extremes of the curve (6–11 cm, 15–23 cm) intersected at approximately 11.5 cm and 20 g. It was at close to this point that parr marks became indistinct and silvering apparent. All ahimals larger than 13.5 cm and heavier than 26 g were judged to have passed the parr stage of development.

As might be expected from the general appearance of this curve, smolt were characterized by lower coefficients of condition than parr. The mean values for the coefficients of condition of all parr, silvery parr and smolt sampled in the investigation were 1.063, 1.009 and 0.949, respectively. Comparable variations in condition factor with developmental stage have been observed by Hoar (1939) and Evropeitseva (1957).

On the basis of evidence of variations in length–weight relationship, decrease in condition factor, and appearance of the morphological features characteristic of smolt the initiation of the transformation process is seemingly markedly size-dependent. The critical lengths and weights for this population appeared

to lie between 11.5 and 13.5 cm, and 18.5 and 26 g. No animals lying below these ranges displayed any of the more obvious features of the smolt, while all animals above them exhibited at least some of the characteristics of the smolt stage of development. Evropeitseva (1957) on the basis of studies on Atlantic salmon populations of the Baltic region gives the lower weight limits for silvery parr and smolt as 10 and 16 g, respectively. These values were, however, observed in an investigation specifically designed to bring on transformation at the earliest possible time. The data also agree reasonably well with Elson's suggested "10 centimeter rule" for the transformation of Atlantic salmon parr into smolt (Elson, 1957), and with Evropeitseva's observation that a weight of 15–17 g must be attained by yearling parr if they are to undergo natural smoltification during their second summer of life (Evropeitseva, 1957). Both studies emphasize the importance of growth-regulating factors in the control of transformation, confirming several observations (see Brown, 1957, for review) that normal seaward migration in the smolting salmonids (which presupposes the completion of this process) is more particularly dependent upon size and rate of growth than upon age.

Water–Electrolyte Regulation during Parr–Smolt Metamorphosis

Plasma chloride

Variations in plasma chloride with weight and stage of development are recorded in Fig. 2 for a sample of 66 salmon, comprising 22 parr, 18 silvery parr

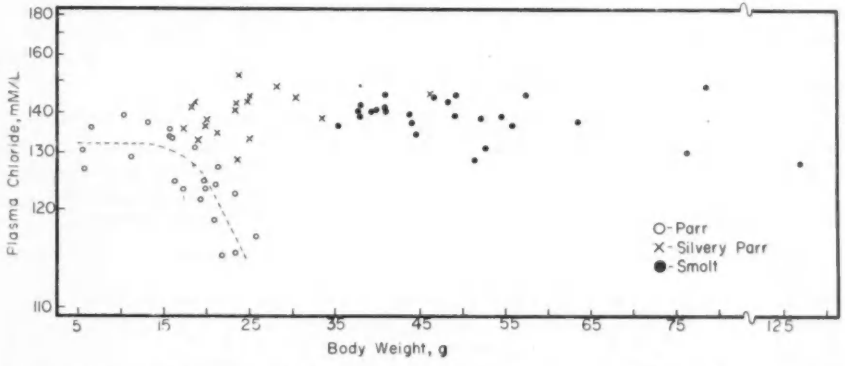

Fig. 2. Variation on plasma chloride concentration with weight and stage of development. Trend lines visually fitted.

and 26 smolt. Values for parr of less than 10 g weight were based upon analyses of pooled samples from two or three animals, and have been related to the mean weight of the contributing fish.

Plasma chloride levels showed considerable variation, ranging from 114.6 to 152.2 m*M*/l. Inspection of these data, however, suggests that two groups may be distinguished with respect to weight-related variations in plasma concentration. In the first group, consisting of fish classified as parr, the smaller animals

(5–15 g) displayed no consistent variation in concentration with weight, and individual values ranged from 126.8 to 139.2 m*M*/l. In larger parr, however, there was a marked drop in plasma concentration, with values falling from the levels cited to a minimum of 114.6–116.7 in the largest animals judged to be of this group.

Among the second group, consisting of silvery parr and smolt, there appeared to be little evidence of a sharp break in the plasma chloride–body weight relationship. Silvery parr (17–36 g) were characterized by plasma chloride values which were somewhat higher than those seen in parr, i.e. 128.8–152.2 m*M*/l. Comparable values were recorded in smolt, and there was no pronounced drop in concentration with increasing weight similar to that seen in the parr.

These data indicate that juvenile Atlantic salmon suffer some loss in ability to regulate plasma electrolyte concentrations at specific levels during parr–smolt transformation. The most marked variation from the population mean of 136.0 m*M*/l occurred among animals judged upon the basis of absence of silvering, presence of distinct parr-marks, and weight to be large parr. A visually fitted trend line through the data for this group suggested that decreases in concentration became pronounced within the 15–18 g weight range. Reference to Fig. 1 indicates that this range falls immediately in front of the point of inflection of the weight–length curve for this population of fish. This, and the fact that depressed chloride levels were characteristic of fish lacking any of the more obvious morphological features characteristic of smoltification supports the suggestion that transformation may be well under way sooner than is generally recognized on the basis of morphological criteria.

Tissue chloride

A somewhat similar variation of tissue chloride content with weight and stage of development may be observed in Fig. 3 in which data for a sample of 66 fish (33 parr, 9 silvery parr, 24 smolt) is recorded. The smallest parr sampled (2.7–3.5 g) had tissue chloride concentrations ranging from 43 to 59 m*M*/kg fresh

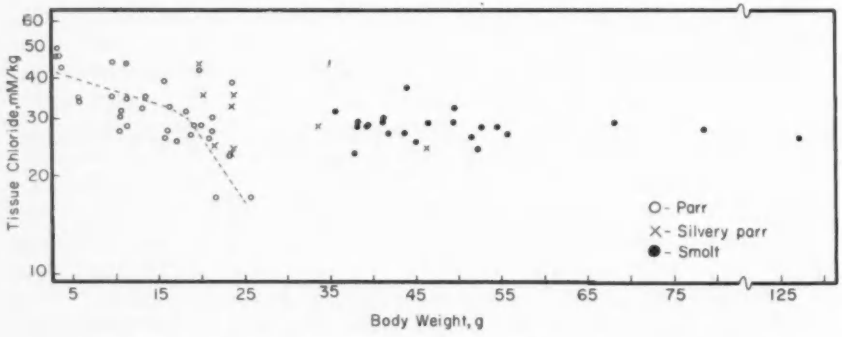

Fig. 3. Variation on tissue chloride concentration with weight and stage of development. Trend lines visually fitted.

tissue. The lowest values observed were two (17.3, 17.4 mM/kg fresh tissue) representing fish in the large parr group. The sharpest deviations from a linear variation of concentration with weight were again found in the 15–20 g weight range. Values for silvery parr and smolt decreased slightly with increasing weight, but with little evidence for a difference within this group comparable to that seen among parr.

Leaving aside the perhaps questionable inflection in values within the parr group it is apparent that tissue chloride does not vary in a regular fashion with weight alone. Considering all data from the three developmental groups a flattening of the concentration versus weight relationship is apparent between 15 and 20 g, that is, within the range characterized by the appearance of morphological smolt characteristics, and the decrease in ability to regulate plasma chloride levels.

Tissue water

Figure 4 includes values for tissue water content in a group of 65 salmon, including 33 parr, 9 silvery parr and 23 smolt. A decrease in tissue water content with increase in weight is apparent, but no pronounced stage-related variations related to smoltification were present.

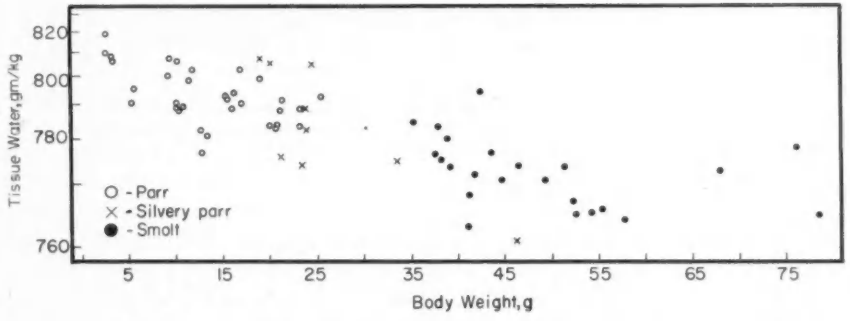

Fig. 4. Variation in tissue water content with weight and stage of development. Trend lines visually fitted.

Chloride space (extracellular phase volume)

Values for chloride space were calculated for 51 animals (20 parr, 8 silvery parr, 23 smolt) for which complete sets of data were available (Fig. 5). Both size- and stage-dependent variations were present. A sharp drop in chloride space with increase in weight was characteristic of parr. By contrast, variations in the chloride space of larger silvery parr and smolt were less marked. The sharpest deviations from linear variation with weight were observed within the weight ranges previously cited, and indicated that a reduction in extracellular phase volume accompanied smoltification.

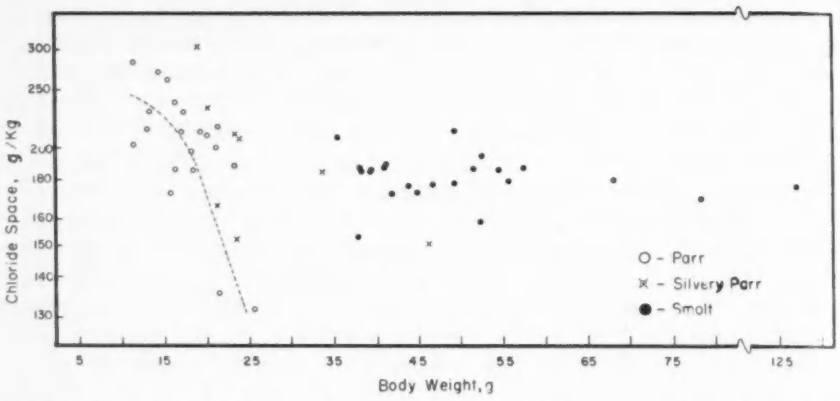

FIG. 5. Variation in chloride space with weight and stage of development. Trend lines visually fitted.

TISSUE WATER MINUS CHLORIDE SPACE (CELLULAR PHASE VOLUME)

Values for tissue water minus chloride space are recorded for a sample of 51 fish (20 parr, 8 silvery parr, 23 smolt) in Fig. 6. As might be expected, allowing for the overall decrease in tissue water content, these values were the mirror image of those for chloride space, and indicated the occurrence of an abrupt increase in the volume of the cellular phase at the commencement of metamorphosis.

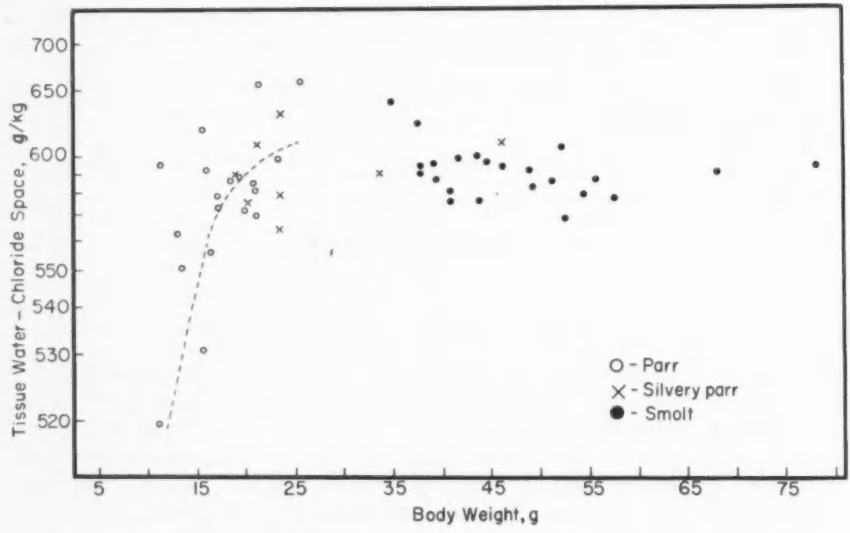

FIG. 6. Variations in cellular volume (tissue water content minus chloride space) with weight and stage of development. Trend lines visually fitted.

DISCUSSION

Electrolyte Regulation during Parr–Smolt Metamorphosis

The values recorded in the present study are generally in agreement with those obtained in earlier studies (Table I). This is particularly so with respect to plasma chloride. Tissue chloride values in the literature tend to be somewhat lower than those reported here, but this may be attributable, in part, to analytical losses attending the commonly employed "open digestion" procedures (Shenk, 1954). The tissue chloride values noted in the smallest parr sampled are well above the highest yet recorded for fishes, but find a parallel in the observations of Barlow and Manery (1954) on the tissue chloride content of young birds and mammals.

Relatively few estimates of extracellular phase volume have been made for fish tissues. However, Nishie and Harris (1955) have reported sodium and chloride spaces in *Electrophorus* comparable to those observed in the present study, and in steelhead trout (Houston, 1959b). Thorson's recent estimates of extracellular phase volume in a variety of teleosts by the sucrose space technique are also in good agreement with values for silvery parr and smolt (Thorson, 1961). Somewhat lower values may be derived from data reported by Chartier-Baraduc (1959) for rainbow trout, and by Gordon (1959a) for brown trout. Data from Fontaine *et al.* (1950) and Fontaine (1951) for *Salmo salar* give values similar to those of Chartier-Baraduc (1959) and Gordon (1959a). The very low value (12.8 ml/kg) for chloride space derived from Parry's data for Atlantic salmon (Parry, 1961) may be attributed to the unusually low value for muscle chloride concentration reported by this author.

Premigratory decreases in plasma electrolyte levels have been observed in *Oncorhynchus masou* (Kubo, 1955) and *Salmo gairdneri* (Houston, 1959b). Fontaine *et al.* (1950) detected only slight variations in Atlantic salmon, although decreases of 22–29% were observed in tissue chloride (Fontaine, 1951). Koch *et al.* (1959) have commented upon an apparent loss in sodium-regulating ability in this species during smoltification.

Variations in tissue water distribution in smolting salmonids have been investigated in the steelhead trout (Houston, 1959b) and were comparable to those noted in Atlantic salmon smolt. Data provided by Fontaine *et al.* (1950) and Fontaine (1951) suggest that a decrease of approximately 14% in extracellular phase volume accompanied smoltification in the Atlantic salmon population studied.

Decreases in extracellular phase volume are characteristic of periods of rapid or differential growth in vertebrates and are, therefore, a not unexpected feature of parr–smolt metamorphosis in salmonids. Fellers *et al.* (1949) have reported decreases of 79% and 57% in thiocyanate and sodium — 24 spaces in humans between infancy and maturity. The neonatal and adolescent periods were particularly noteworthy for rapid changes in extracellular phase volume. Similar variations have been encountered in the laboratory rat and domestic chicken (Barlow and Manery, 1954). Newly hatched chicks, for example, had chloride

TABLE I. Representative values for plasma and tissue chloride, chloride space and cellular phase volume in freshwater-adapted salmonids.

Species	Plasma chloride m*M*/l	Tissue chloride m*M*/kg	Chloride space ml/kg	Cellular space ml/kg	Remarks	Reference
S. salar	123.1				parr	Fontaine *et al.*, 1950
	122.6				smolt	Fontaine *et al.*, 1950
		8.8			parr	Fontaine, 1951
		7.3			smolt	Fontaine, 1951
			61.3			Calculated from data in Fontaine *et al.*, 1950, and Fontaine, 1951
			12.8			Parry, 1961*
S. trutta	119.4					Field *et al.*, 1943
	129.2 ± 1.3	8.2 ± 0.3	64 (59–68)		20°C	Gordon, 1959a
	130.0 ± 1.3	7.8 ± 0.5	62 (52–72)		10°C	Gordon, 1959a
	133.3 ± 3.1					Gordon, 1959b
S. gairdneri	111 ± 3.9	10.5 ± 0.32	85.1	705.5		Chartier-Baraduc, 1959
	Y = 152.8–0.30*x***	*Y* = 31.9–0.18*x*	*Y* = 217.1–1.28*x*	*Y* = 628.3+0.43*x*	25–70 g	Houston, 1959b
	Y = 141.0–0.04*x*	*Y* = 14.9–0.02*x*	*Y* = 103.4–0.16*x*	*Y* = 619.2–0.02*x*	70–250 g	Houston, 1959b

*Calculated from text data.
**x = weight in grams.

spaces averaging 514 ml/kg and cellular spaces averaging 313 ml/kg. Comparable values for mature birds were 70 and 671 ml/kg. Medway and Kare (1959) observed that thiocyanate space dropped from a value of 61% of body weight in one-week-old chicks to 26% in adult birds. Thus, the variations in tissue water distribution observed in this study to accompany smoltification, while large, are not without parallel among the vertebrates.

Physiological Basis of Variations in Regulatory Ability Occurring during Parr–Smolt Metamorphosis

The changes in inorganic ion levels and tissue water distribution which take place during parr–smolt metamorphosis may be assumed to reflect modifications in water–electrolyte metabolism which presumably preadapt the animals to marine life. Some insight into their physiological basis may be gained through consideration of the osmoregulatory processes employed by freshwater and marine teleosts. The regulatory problems of these animals are clearly understood, and have recently been well reviewed (Black, 1957). Freshwater teleosts rely principally upon the production of a voluminous, hypotonic urine and active absorption of ions to overcome osmotic overhydration and urinary and other forms of salt loss, and achieve water–electrolyte balance. Such processes are obviously inappropriate for life in a medium where osmotic dehydration and salt-loading constitute the central osmoregulatory problems. Under such circumstances body fluid regulation is usually achieved through ingestion of water, restriction of urine production and extrarenal salt excretion.

In the present study there was no evidence suggesting that osmoregulatory preadaptation involved a decrease in urine output, or any other form of water conservation process. An adaptive oliguria comparable to that seen in marine teleosts, would lead to a dilution of body fluid electrolytes, as observed, through uncompensated endosmosis. However, the absence of increases in tissue water content, which would be a consequence of such a process, obviates this possibility. The variations in tissue water levels which do accompany smoltification would, if anything, tend to be reflected by moderate increases in plasma and tissue electrolyte levels.

On the other hand a case may be made for the likelihood of a premigratory increase in the activity of extrarenal electrolyte excretion. The observed decreases in plasma and tissue chloride concentration as seen among parr would be an immediate consequence of such a phenomenon, while the noted variations in the relative volumes of the extracellular and cellular phases may also be accounted for in terms of the activation of the extrarenal salt excretion process. Excretion of inorganic electrolytes from the blood would tend to lower the osmotic concentration of the extracellular fluid. A comparable lowering of cellular fluid osmolarity would not be expected. The major extracellular ions, sodium and chloride, are in low concentration within cells, while a large fraction of cellular inorganic electrolyte exists in the bound state (Conway, 1957). Moreover, much of the osmotically active material of cellular fluid is organic and non-diffusible. Thus, a tendency toward cellular hyperosmolarity would accompany

electrolyte excretion, and in the alleviation of this, the spontaneous osmotic movement of water from the extracellular to the cellular phase. In consequence extracellular phase volume would decrease while that of the cellular phase increased.

In discussing the remaining feature observed in this study, the secondary rise in plasma chloride seen with the attainment of the silvery–parr stage, reference may be made to a correlative study made simultaneously on the Keys-Willmer or "chloride-secretory" cells of these animals with the electron microscope (Threadgold and Houston, 1961, 1963). These branchial cells were described initially by Keys and Willmer (1931) who tentatively linked them to the process of branchial ion excretion earlier demonstrated by Smith (1930) and Keys (1931). Their actual participation in this process remains as yet unestablished, and has recently been contested (Parry *et al.*, 1959; Doyle and Gorecki, 1961; Holliday and Parry, 1962; Straus, 1963; Fleming and Kamemoto, 1963) on a variety of bases. Nevertheless, considerable indirect evidence can be marshalled to support the "ion-secretion" hypothesis. In earlier studies with the light microscope Copeland (1945, 1950), Pettengill and Copeland (1948) and Getman (1950) demonstrated adaptive changes in the form and enzymatic activity of these cells in fish experimentally transferred between fresh and salt water. More recently Philpott (1961, 1962) and Kessel and Beams (1962) have substantiated these findings with electron microscope studies. Copeland (1948, 1950) and Columbo (1960) have histochemically demonstrated the accumulation of chloride in these cells in seawater-adapted *Fundulus* and *Anguilla*. Threadgold and Houston (1961) have correlated apparent increases in secretory activity with heightened plasma chloride levels of Atlantic salmon adapting to sea water. Liu (1942) and Morris (1958) have convincingly correlated the ability of *Micropodis* and *Lampetra* to survive in sea water with the abundance and maturity of such cells. Finally the ontogenetical appearance of "chloride cells" in the anadromous *Salmonidae* (Hoar, 1951; Nishida, 1953; Parry, 1958, 1960) is closely related to the development of tolerance for increased salinity (Huntsman and Hoar, 1939; Black, 1951; Parry, 1958).

The nature of the studies cited indicates that a definitive answer to the question of "chloride cell" function cannot, as yet, be given. However, the adaptive changes in activity observed to occur in these cells in response to increased salinity, and more particularly the good correlation between their occurrence and ability to adapt to sea water can only be taken as favouring the ion-secretory hypothesis. If this conclusion can be accepted as reasonable many of the variations in water–electrolyte balance accompanying smoltification can be accounted for. These cells become abundant during the metamorphic process. Thus, their activity may produce the decreases in plasma and tissue chloride levels observed, as noted earlier. The secondary increase in blood electrolyte concentration may then be attributable to a secondary decrease in "chloride cell" activity. Evidence supporting this hypothesis has been observed both in parr and smolt in the study referred to earlier (Threadgold and Houston, 1963). Among the cells identified in parr as "chloride-secretory" in type many were

classified as *degenerate* or *post-adult*. Such cells exhibited one or more of the following features: (1) vacuolization of mitochondria accompanied by fragmentation of mitochondrial cristae; (2) vacuolization of the Golgi apparatus; (3) cytoplasmic degeneration, and (4) formation of cytoplasmic inclusion bodies. No such degenerate cells were observed among smolt. Many of the "chloride cells" in animals in this stage of development were, however, categorized as *inactive* in type. These cells could be readily distinguished from cells believed to represent the *active* stage of development on the basis of several features including the integrity of mitochondrial structure, abundance of endoplasmic reticulum, absence of apically positioned cytoplasmic microvesicles, and the degree of contact of the apical plasma membrane with the free branchial surface. Again, assuming the validity of the ion-secretory hypothesis these observations may be taken as supporting the hypothesis that the rise in plasma ion levels in silvery parr and smolt represents suppression of the extrarenal salt excretion mechanism.

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On the Problem of Maximum Yield from North Pacific Sockeye Salmon Stocks[1]

By Robert R. Parker

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

If it is assumed that rates of exploitation, regardless of where fishing takes place, can be adjusted to the needs for reproduction, maximum yield from stocks of north Pacific sockeye salmon (*Oncorhynchus nerka*) will then be a function of growth and natural mortality rates. Events during the last decade have demonstrated the vulnerability of this species to pelagic fishing during the penultimate and ultimate years of life. The instantaneous growth rate on a per-month basis (g) is estimated from diverse data by back calculation, tag and recapture, and size-at-time methods. A general consistency of results is apparent regardless of the method utilized. For 2-ocean annuli life history types, penultimate $\bar{g} = 0.105$, ultimate $\bar{g} = 0.111$. For 3-ocean annuli types, penultimate $g = 0.059$, ultimate $\bar{g} = 0.075$. Ocean mortality models and rates derived by several researchers are reviewed and discussed. Using those proposed by the author, it is shown that the stock mass, hence the allowable yield, increases throughout the penultimate and ultimate years in the sea and reaches a maximum when the stocks approach the coast on the spawning migration. A conservative estimate of the potential increment, based on the 1957–1959 pelagic catches, is 14.2%. It is concluded that the yield of these stocks is seriously depressed by pelagic fishing.

INTRODUCTION

Events during the last decade have demonstrated the vulnerability of sockeye salmon (*Oncorhynchus nerka*) to fishing conducted on the high seas. During this time oceanic fisheries have been active from mid May into August and because of the variable life history of this species sockeye were taken in both the penultimate and ultimate years of life[2]. If it is assumed that the intensity of fishing, irrespective of where it takes place, can be adjusted to the needs for reproduction, the yield will then be a function of growth and mortality during the penultimate and ultimate years.

Four studies of this problem, specifically for sockeye, have recently become available. Taguchi (1961b) concluded that during the last 2 months of the ultimate year sockeye stock weight decreases. Yamanaka (1963) concluded the catching of non-ultimate year sockeye by the pelagic fishery increased the possible yield from the stock. Ricker (1962) concluded that the stock weight increases during both the penultimate and ultimate years. Fredin (MS, 1963) concluded that pelagic fishing for Karluk sockeye causes a loss in potential yield. It is

[1]Received for publication August 20, 1963.

[2]Mr J. Manzer, Fisheries Research Board of Canada Biological Station, Nanaimo, states that the pelagic commercial fisheries take very few fish less than 45 cm fork length. We will, then, confine the arguments which follow to fish in their penultimate and ultimate years.

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the purpose of this communication to examine this question further using data presented by the above authors, those of some recent studies which have become available, and those of some older studies which have not as yet been used in the arguments.

GROWTH ESTIMATES

Growth in time may be estimated by three independent methods. (1) From a known or assumed body–scale relationship, lengths at various life-history events may be estimated from measurements of scales. This method is popularly called "back calculation". (2) A population of fish may be repeatedly sampled in time and average growth rate deduced by comparing size frequencies. (3) Individuals may be tagged and later recovered yielding growth data for the period of freedom. All of these methods have certain practical and theoretical advantages and disadvantages which will be discussed after presentation of growth estimates. Data are now available from which growth of sockeye in the North Pacific may be estimated by each method.

Length–Weight Relationship

Most of the size data to be considered are reported in terms of body (fork) length and it is necessary to define the relationship between length and weight for sockeye in the sea. Lander and Tanonaka (MS, 1962, table 10) present mean fork lengths and body weights for western Alaska sockeye captured in the Aleutian area. Natural logarithms (Ln) of mean weight in kilograms (Ln $\overline{w}$) are plotted as a function of natural logarithms of mean fork length in decimeters (Ln $\overline{l}$), irrespective of life history type of stage, sex, or calendar time, in Fig. 1. The distribution is obviously linear and the computed regression of Ln $\overline{w}$ = f(Ln $\overline{l}$) is

$$\text{L}n\ w = \overline{5}.1677 + 3.2666\ \text{L}n\ \overline{l} \qquad (1)$$

Equation (1) will be used throughout this paper in converting average lengths into equivalent Ln $\overline{w}$.

Instantaneous Growth Rates

Instantaneous growth rates (g) are estimated from the relationship

$$g = (\text{L}n\ \overline{w}_t - \text{L}n\ \overline{w}_0)/t \qquad (2)$$

where t in units of one month denotes the time interval. The time interval between annuli formation is assumed to be 12 months. In the ultimate growth year t varies among the stocks considered, but is taken to represent the period (in months) from April 1 to the best estimate of the approach of the stock to the spawning river estuary. In this paper g is given on a per-month basis.

Cultus and Karluk Sockeye

Ricker (1962) presented estimates of instantaneous growth rates for Cultus (British Columbia) and Karluk (Alaska) sockeye stocks. Using data for Cultus sockeye of Foerster and for Karluk sockeye of Barnaby, lengths at the end of scale annuli formation, derived by back calculation, were converted to weights

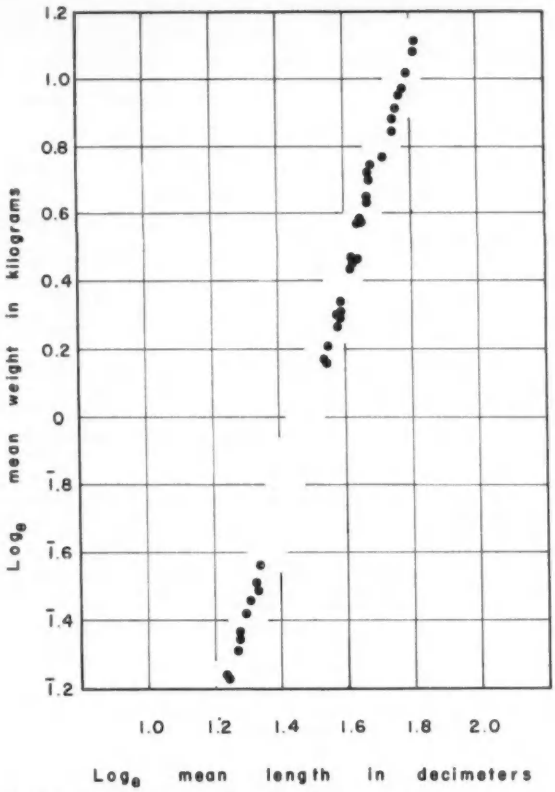

FIG. 1. The relationship between $Ln\ \bar{l}$ and $Ln\ \bar{w}$ for western Alaska sockeye (data from Lander and Tanonaka, MS, 1962).

by a length–weight relationship for Cultus sockeye smolts. For the present study, average calculated lengths presented by Ricker in his appendix table B for the 1/2[3] and 2/2 life-history types of the Cultus stock and the 2/2 and 3/2 types of the Karluk stock have been combined into weighted average lengths at the end of the antepenultimate, penultimate, and ultimate growth years to represent the 2-ocean annulus growth type. These data and the subsequent treatment are presented in Table I. Using equations (1) and (2), values of $Ln\ \bar{w}$ and g are calculated as presented in Table II. Values of g given in Table II differ but little from those given by Ricker in his table I.

DALNEE SOCKEYE

Krogius (1960, table 6) presented similar data for male Dalnee (E. Kamchatka) sockeye from the 1942–1951 spawning runs. Average lengths for 2-

[3]This designation of 1 fresh-water annulus/2 ocean annuli is equivalent to 4_2 of the Gilbert system, and 3_1 as used by many Asian scientists.

TABLE I. Average fork lengths in decimeters of Cultus and Karluk sockeye[a].

Stock	Life history	n	Length at end of growth year		
			Antepenultimate	Penultimate	Ultimate
Cultus	1/2	40	3.55	5.27	6.20
	2/2	16	3.73	5.46	6.15
Weighted average:			3.601	5.324	6.186
Karluk	2/2	22	3.26	4.99	5.64
	3/2	17	3.71	5.15	5.66
Weighted average:			3.456	5.060	5.649

[a]Data from Ricker, 1962, appendix table B.

TABLE II. Estimates of size at age and growth rates of Cultus and Karluk sockeye.

Year of life	Size	2-ocean annuli	
		Cultus	Karluk
Antepenultimate	$\bar{l}$	3.601	3.456
	$Ln\ \bar{l}$	1.2812	1.2401
	$Ln\ \bar{w}$	$\bar{1}$.3521	$\bar{1}$.2179
Penultimate	$\bar{l}$	5.324	5.060
	$Ln\ \bar{l}$	1.6722	1.6214
	$Ln\ \bar{w}$	0.6291	0.4632
	g	0.106	0.104
Ultimate[a]	$\bar{l}$	6.186	5.649
	$Ln\ \bar{l}$	1.8223	1.7315
	$Ln\ \bar{w}$	1.1193	0.8228
	g	0.102	0.154

[a]Ultimate growth year for Cultus sockeye was approximately April 1 to August 25 or 4.8 months. For Karluk data it was approximately April 1 to June 10 or 2.3 months.

TABLE III. Average fork lengths in decimeters of male Dalnee sockeye[a].

Life history type	Length at end of growth year		
	Antepenultimate	Penultimate	Ultimate
1/2	3.18	4.71	5.37
2/2	3.68	5.06	5.58
Average:	3.430	4.885	5.475
1/3	4.24	5.31	5.78
2/3	4.45	5.35	5.76
Average:	4.345	5.330	5.770

[a]Data from Krogius, 1960, table 6.

TABLE IV. Estimates of size at age and growth rates of male Dalnee sockeye.

Year of life	Size	Life history type: 2-ocean annuli	Life history type: 3-ocean annuli
Antepenultimate	$\bar{l}$	3.430	4.345
	$Ln\ \bar{l}$	1.2326	1.4690
	$Ln\ \bar{w}$	$\bar{1}$.1934	$\bar{1}$.9655
Penultimate	$\bar{l}$	4.885	5.330
	$Ln\ \bar{l}$	1.5862	1.6734
	$Ln\ \bar{w}$	0.3482	0.6330
	g	0.096	0.056
Ultimate[a]	$\bar{l}$	5.475	5.770
	$Ln\ \bar{l}$	1.7002	1.7572
	$Ln\ \bar{w}$	0.7206	0.8920
	g	0.093	0.065

[a]Ultimate growth year approximately April 1 to August 1 or 4 months.

ocean annuli type are obtained by averaging data for the 1/2 and 2/2 life-history types. Average lengths for the 3-ocean annuli type result from averaging data presented for the 1/3 and 2/3 life-history types. These data and their treatments leading to estimates of $Ln\ \bar{w}$ and g are presented in Tables III and IV.

KURILE SOCKEYE

Size data to represent Kurile sockeye are available from two sources. Krokhin and Krogius (1937, tables 49 and 52) provide estimates of lengths at age for life-history groups and sexes comprising the 1930 spawning run. These have been combined into weighted average lengths at age for 2- and 3-ocean annuli types. Treatment of these data and steps leading to estimates of g are given in Table V.

Hanamura (1961, table 20) presented data (credited to Egorova, 1960, unpublished MS) from which average lengths at age derived by back calculation of scale samples taken from 1944–1950 Kurile sockeye spawning runs are available. These average lengths, together with estimates of g, are presented in Table VI.

ALEUTIAN AREA SOCKEYE

Taguchi (1961a) estimated growth rates using data of Hartt (1962) on lengths at tagging and recapture of sockeye in the Aleutian area. Instantaneous growth rates in length were converted to those of weight by multiplication with the exponent 3.6 to 3.7 of the length-weight expression which he used. Taguchi's estimates are the equivalent, on a per-month basis, of $g = 0.061$ for fish recaptured in the year following tagging and $g = 0.171$ for fish recaptured during the year of tagging. I have not been able to reproduce his results from the data sources cited primarily because no mention is made of which data were used in the

TABLE V. Estimates of size at age and growth rates for 1930 spawning group Kurile sockeye[a].

Mid point of length interval (decimeters)	Size frequency at end of growth year					
	2-ocean annuli			3-ocean annuli		
	Antepenultimate	Penultimate	Ultimate[b]	Antepenultimate	Penultimate	Ultimate[b]
2.55	4					
2.75	6					
2.95	18					
3.15	12			1		
3.35	10			2		
3.55	4			1		
3.75	3	1		3		
3.95	0	3		14		
4.15	1	2		31		
4.35		9		37		
4.55		20		26	3	
4.75		7	2	16	4	
4.95		12	7	5	19	
5.15		1	8	2	36	5
5.35		1	16		29	13
5.55		2	32		29	46
5.75			17		17	56
5.95			11		2	48
6.15			3			23
6.35			3			17
6.55						4
6.75						1
Average length ($\bar{l}$)	3.116	4.626	5.548	4.340	5.308	5.824
$Ln\ \bar{l}$	1.1366	1.5317	1.7134	1.4679	1.6692	1.7620
$Ln\ \bar{w}$	$\bar{2}.8797$	0.1702	0.7638	$\bar{1}.9618$	0.6194	0.9223
g		0.108	0.132		0.055	0.067

[a]Based on data of Krokhin and Krogius, 1937, tables 49 and 52.
[b]Ultimate growth year from April 1 to August 15 or 4.5 months.

TABLE VI. Estimations of size at age and growth rates of Kurile sockeye, 1944–1950 spawnings[a].

Year of life	Size	Life history type: 2-ocean annuli	Life history type: 3-ocean annuli
Antepenultimate	l	3.003	4.495
	$Ln\ l$	1.0996	1.5030
	$Ln\ \bar{w}$	2.7590	0.0765
Penultimate	l	4.728	5.585
	$Ln\ l$	1.5535	1.7201
	$Ln\ \bar{w}$	0.2414	0.7855
	g	0.124	0.059
Ultimate[b]	l	5.253	5.898
	$Ln\ l$	1.6588	1.7746
	$Ln\ \bar{w}$	0.5853	0.9635
	g	0.076	0.040

[a]Based on data presented by Hanamura, 1961, table 20.
[b]Ultimate growth year from April 1 to August 15 (4.5 months).

computations. Numbers of usable sets of measurements were quite small, however, for in Taguchi's table I the number of recoveries listed for the year of tagging is given as 21, and for recoveries during the following year as 19.

Much more data have become available in INPFC[4] Document Nos. 335 (1), 451, 525 and 567 which, together with Hartt's (1962) report, give lengths at tagging and recapture of FRI[5] tagging experiments in the Aleutian area for the years 1957 through 1962. Using the criteria of rejecting all shore recoveries[6], 178 usable sets of measurements are available as listed in Appendix A and B.

Ocean ages may be roughly distinguished by including all fish less than 40 cm fork length at tagging with the 1-ocean annulus group. There are, then, 13 sets to represent 2-ocean annuli and 44 sets to represent 3-ocean annuli fish during their penultimate years[7]. Recoveries during the year of tagging represent a mixture of 2- and 3-ocean annuli types primarily maturing. There are 121 usable sets of measurements for this category.

It is known that length measurements taken on the same fish when alive and dead will differ, the latter measurement usually being the longer if taken immediately after death and before rigor mortis (Parker, 1962b). Before calculating

[4]International North Pacific Fisheries Commission, Vancouver, B.C.

[5]Fisheries Research Institute, University of Washington, Seattle Washington.

[6]Most of the tagged fish recovered by the Japanese pelagic fishery were measured by trained fishery workers. This was not the case for lengths reported from recoveries in the American shore-based fishery. Furthermore, there is no way of knowing how much time individual fish taken by shore-based fisheries or on the spawning grounds had spent in the estuaries or streams maturing under non-feeding conditions.

[7]A small portion of these fish may have been 4-ocean annuli type in their antepenultimate year.

growth rates from these sets of data it was first necessary to estimate and remove this bias. Previous work (Parker and Larkin, 1959) has suggested that chinook salmon (*O. tshawytscha*) and steelhead trout (*Salmo gairdneri*) tend to grow by approximately constant annual length increments after the very small stages[8]. If it can be assumed that this type of growth is appropriate for sockeye, then a plot of $\Delta l = f(\Delta t)$ should be linear on an annual basis. Segmenting this relationship into shorter time periods may disclose departures from linearity because of the intra-seasonal pattern of accelerating spring and decelerating fall growth. Within any particular short period of time, however, this may still be a useful approximation. These data are subject to additional sources of error associated with measuring and recording as well as actual variation in growth increments among the individuals. The former may account for extreme and negative values of Δl and undoubtedly obliterates the latter, however both are probably without bias, i.e. lead to a normal distribution of Δl about a regression line. The average bias caused by measurements taken first from live and then from dead fish would, therefore, be measured as the zero intersect of the regression line of $\Delta l = f(\Delta t)$ and is expected to be positive in this situation. A plot of $\Delta l = f(\Delta t)$ for the 121 sets of year-of-tagging returns is presented as Fig. 2. The fitted regression line intersects the $\Delta t = 0$ ordinate at 9.01 mm which estimates the average value of this measurement bias.

The slope of the function, which is the required statistic for estimating growth rate, is $b = 0.0444$ cm/day. Fish were tagged as early as May 18 and recovered as late as August 9, a period of 83 days. The average length of 61 fish tagged during the period May 31 to June 9 was 5.39 decimeters[9]. Converted into the natural logarithm of average weight, $Ln\ \bar{w} = 0.6709$ to apply to June 5, the midpoint of that period of tagging. A second point was calculated for August 9, 65 days later, by the slope 0.444 mm/day to obtain the average size, $\bar{l} = 5.68$ decimeters, $Ln\ \bar{w} = 0.841$. A third point was calculated for May 18, 18 days prior to June 5, $\bar{l} = 5.31$, $Ln\ \bar{w} = 0.621$. The estimate for growth during the 2.76-month (83-day) period May 18 to August 9 is, then,

$$g = (0.841 - 0.621)/2.76 = 0.080.$$

For 3-ocean annuli fish recovered the year after tagging the average size at tagging was 4.60 decimeters and $Ln\ \bar{w} = 0.151$. The average date of tagging was July 19. Average time free was 10.9 months. The average length increment, corrected for alive and dead measurement bias, was 0.97 decimeters. On the average, then, fish were recaptured on June 10 at $\bar{l} = 5.57$ decimeters, $Ln\ \bar{w} = 0.775$, and

$$g = (0.775 - 0.151)/10.9 = 0.057.$$

[8]A value of $Z = 1.3$ was obtained for chinook in the sea. The growth line thus approaches 45° in a Walford plot so that after 15–20 cm growth is effectively linear. For steelhead in the sea $Z = 1.0$, i.e. growth in length is by constant increments per unit time.

[9]More strictly, this average length should have the average bias of live measurement, 0.09 decimeters subtracted from it so that $\bar{l} = 5.30$ decimeters. This does not affect the growth rate argument, however, and I have left it as a "measured alive" length.

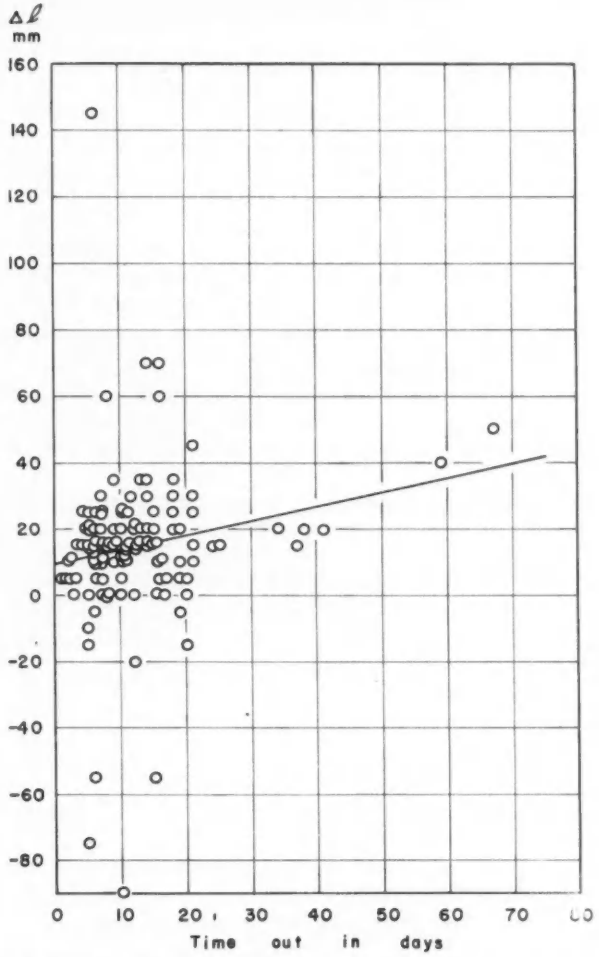

FIG. 2. The relationship between size at tagging and at recapture during the year of tagging, North Pacific sockeye (data from Hartt, 1962, and I.N.P.F.C. Documents 335(1), 451, 525, and 567).

Similarly, the 13 sets of data representative of penultimate year growth for 2-ocean annuli type sockeye lead to the following estimates:

At tagging:

Average date = July 24
Average length = 3.69 decimeters
L*n* average weight = $\bar{1}.433$

At recovery:

Average date = June 11
Average Δl, corrected = 1.08 decimeters
Average length = 4.77 decimeters
Ln average weight = 0.272
Average time out = 10.6 months
g = 0.079

WESTERN ALASKA SOCKEYE

Lander and Tanonaka (MS, 1962, tables 10, 12 and 13) have presented size at time data and calculated average instantaneous growth rates for western Alaska sockeye. Starting with their average weights in time (Lander and Tanonaka, MS, 1962, table 10) I have combined sexes to estimate average weights of sockeye during 10-day time periods as shown in Table VII. Calculations leading to estimates of g are detailed in Table VIII where the results are compared with those of Lander and Tanonaka, arrived at by slightly different reasoning. Differences in method had little influence on the results.

TABLE VII. Average weights (kg) at time for western Alaska sockeye, sexes combined[a].

	Penultimate year		Ultimate year	
Mid date of 10-day period	2-ocean annuli	3-ocean annuli	2-ocean annuli	3-ocean annuli
May 26			1.756	2.483
June 5			1.899	2.582
June 15			1.924	2.720
June 25			1.948	2.818
July 5		1.242	2.024	
July 15	0.485			

[a]Based on data from Lander and Tanonaka, MS, table 10.

DISCUSSION OF GROWTH RATE ESTIMATES

Estimates developed in this text, those of Taguchi (1961a), of Ricker (1962), and of Lander and Tanonaka (MS, 1962), are compared in Table IX. In Fig. 3, Ln $\overline{w}$ values are plotted as a function of time so that sizes and periods of observation may be compared. The instantaneous growth rates may be compared by observing the slopes of regression lines. A notable feature of this comparison is that the results are quite similar regardless of the method used to produce them.

Deriving lengths at the end of annulus formation by back calculation has the advantage that stocks and life-history types are not mixed. There may be some error in the various body:scale relationships used, but trial calculations suggest it could not be serious. It is also assumed that the annuli are completed

TABLE VIII. Natural logarithms of weight at time for western Alaska sockeye, sexes combined and estimates of instantaneous growth rate[a].

Mid date of 10-day period	Penultimate year		Ultimate year	
	2-ocean annuli	3-ocean annuli	2-ocean annuli	3-ocean annuli
May 26			0.5627	0.9095
June 5			0.6413	0.9487
June 15			0.6546	1.0006
June 25			0.6666	1.0362
July 5		0.2163	0.7048	
July 15	$\bar{1}$.2764			
g	0.122[b]	0.070[e]	0.107[d]	0.127[c]

[a]Based on data from Lander and Tanonaka, MS, table 10.
[b]$g = (0.7048 - \bar{1}.2764)/11.67$
[e]$g = (1.0362 - 0.2163)/11.67$
[d]$g = 3/4[(0.7048 - 0.666) + (0.666 - 0.6546) + (0.6546 - 0.6413) + (0.6413 - 0.5627)]$.
[c]$g = (1.0362 - 1.0006) + (1.0006 - 0.9487) + (0.9487 - 0.9095)$.

TABLE IX. Comparison of estimates of instantaneous growth rates for North Pacific sockeye stocks. Methods of estimation were: A — back calculation from scale annuli; B — recovery of tagged fish; C — progressive sampling of the stock at sea.

Source	Method	Penultimate year			Ultimate year		
		2-ocean annulus	3-ocean annulus	2 + 3 ocean	2-ocean annulus	3-ocean annulus	2 + 3 ocean
This paper							
1. Cultus	A	0.106	...	...	0.102	...	...
2. Karluk	A	0.104	...	...	0.154	...	...
3. Kurile (1930)	A	0.108	0.055	...	0.132	0.067	...
4. Kurile (1944–1950)	A	0.124	0.059	...	0.076	0.040	...
5. Dalnee	A	0.096	0.056	...	0.093	0.065	...
6. FRI tagging	B	0.076[d]	0.057[d]	...	...	...	0.079[e]
7. Western Alaska	C	0.122[d]	0.070[d]	...	0.107[e]	0.127[e]	...
Average:	...	0.105	0.059	...	0.111	0.075	...
Average excluding 6:	0.110	0.060	...	...	...	...	...
Cited from the literature							
8. Cultus (average, 1/2)[a]	A	0.110	...	...	0.102	...	...
9. Karluk 2/2[a]	A	0.105	...	...	0.156	...	...
10. Karluk 3/2[a]	A	0.081	...	...	0.121	...	...
11. Aleutian area[b]	B	...	...	0.061[d]	...	...	0.171[e]
12. Western Alaska[c]	C	0.12[d]	0.06[d]	...	0.09[e]	0.13[e]	...

[a]Ricker, 1962, tables I and II.
[b]Taguchi, 1961a, table 2.
[c]Lander and Tanonaka, MS, tables 12 and 13.
[d]Based on about 8 months penultimate year + 3 to 4 months ultimate year growth.
[e]Based on about 30–40 days of summer growth.

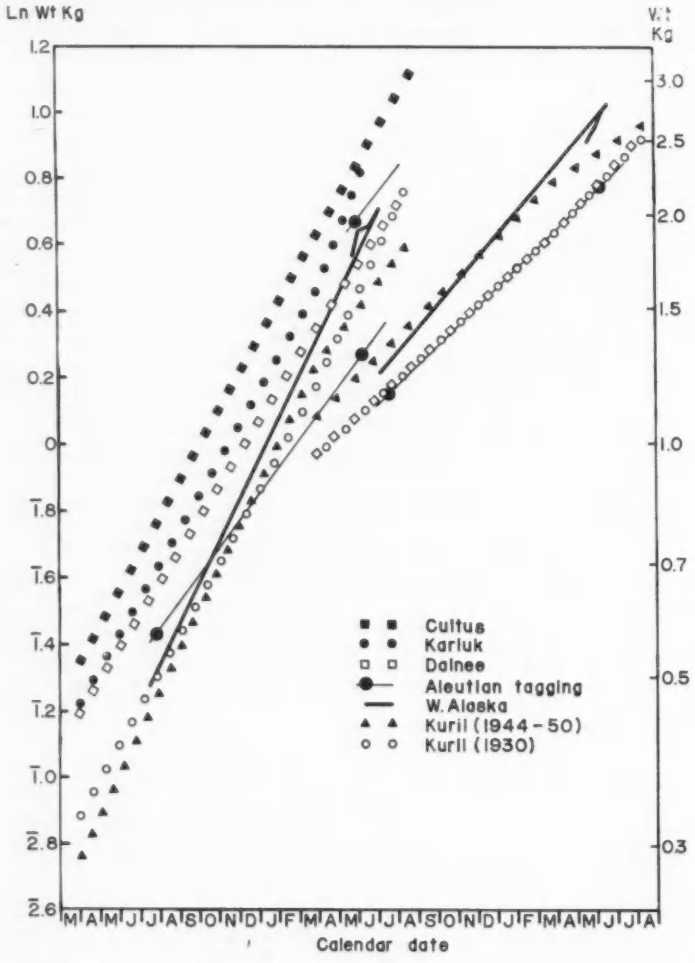

FIG. 3. The relationship between $L\bar{n}\ \bar{w}$ and time, for North Pacific sockeye in the penultimate and ultimate years.

at exactly 12-month intervals, which may not be strictly true, but again possible deviations could not cause much error. A more important source of error may result from uncertainty regarding the duration of the actual growth period during the ultimate year. This alone might account for differences in ultimate year growth rate between stocks noted in Table IX and Fig. 3.

Growth rates as derived from length frequencies taken consecutively in time are without some of these objections, but in an area as large as that from which Lander and Tanonaka's data were obtained it is not certain that all of the samples

were drawn from a population with a uniform growth history. Hence it is likely that some of the short-term negative growth periods (Lander and Tanonaka, MS, 1962, fig. 17) merely reflect the movements of groups of fish of different growth histories within the area sampled.

Growth rates derived from measurements of tagged fish do not have the above objections, but require the assumption that growth is unaffected by the tag and the tagging procedure. Fish recovered during the year after tagging could not be classified with certainty as being in their ultimate year, though the great majority were so. Recoveries during the year of tagging likewise were a mixture of fish in their penultimate and ultimate years. More serious, perhaps, fish tagged and recovered during the year following tagging were free for only 10.6–10.9 months (averages for 2- and 3-ocean annuli). More than one month of the fast growing season is, therefore, not included in the estimates of g from these data; hence the monthly growth rate obtained is less than the average rate over a full year.

In spite of these weaknesses, the results of the various approaches are quite similar (Table IX). For 2-ocean annuli types in the penultimate growth year values of g ranging from 0.076 to 0.124 have been computed. The mean of these values is $\bar{g} = 0.105$. If the tagging figures, which are known to be biased in the direction of being too small, are disregarded the average is 0.110. For the ultimate growth year, values of g ranging from 0.076 to 0.154 have been computed. The mean of these values is $\bar{g} = 0.111$. For 3-ocean annuli sockeye in their penultimate year, values of computed g range from 0.055 to 0.070; mean $g = 0.059$ (0.060 excluding tagging data). For the ultimate growth year values of computed g range from 0.040 to 0.127; average $g = 0.075$. We may use these average estimates of instantaneous growth rate in weight on a per month basis as generally applicable to both Asian and North American stocks.

MORTALITY ESTIMATES

Of the two parameters, growth and mortality, the latter is the most elusive from the standpoint of available data. Parker (1962a) presented a conceptual model for describing marine mortality of Pacific salmon. Ocean mortality rate (q) was taken as the base to which coastal mortality rates of juveniles (c) and adults (k) were additive factors. The effect of marking was taken as a coefficient (m) of the instantaneous rate (i) where $i = q + c + k$. Together with time these values were incorporated into the equation,

$$c + k = \frac{1}{m}\left[\mathrm{L}n\mathrm{N}_0\text{–}\mathrm{L}n(\mathrm{R}_1 e^{mi_{0.1q}} + \mathrm{R}_2 e^{mi_{0.2q}} + \mathrm{R}_3 e^{mi_{0.3q}} + \cdot +)\right] \qquad (3)$$

Where N_0 denotes any smolt population entering the sea, R_1, R_2, R_3 denote adult returns to the coast in succeeding years of maturity. It is assumed that ocean mortality rate is constant once the salmon are off shore regardless of size.

Data were available from several stocks, both Asian and North American, and for several species of *Oncorhynchus*. The locus of $c + k = f(q)$ was used to depict all possible combinations of $c + k$ and q within the limits $[q, c + k = 0]$ as dictated by observed survivals of smolts to adults. Intersections of loci within

the limit area were interpreted as best estimates of $c + k$ and q. It was concluded that ocean natural mortality rate (q) is relatively constant between the stocks and species and is of the magnitude $q \simeq 0.316$ annually or on a per month basis $q \simeq 0.026$. In terms of survival this is equivalent to 73% per year. A juvenile coastal factor (c) apparently exists and is characteristic of the species and race presumably through the media of size and other factors relating to ecology and physiology of juveniles at entrance into salt water, time spent in the coastal area and geography of the migration routes. An adult coastal factor was estimated as $k \simeq 0.009$ on a per month basis from the relationship of mortality rates of chinook salmon to the average oceanic rate. While those data utilized were considered collectively as extensive, serious defects in sampling errors and undefined variability were encountered leading to uncertainty in the interpretation of intersections of loci.

Because of this uncertainty Ricker (1962) used, as a maximum estimate of q, a value equivalent to limit q where $c + k = 0$, derived from Karluk 3-freshwater annuli sockeye. This rate $q = 0.46$ per annum or $q = 0.038$ on a per month basis is equivalent to a survival of 63% annually. Ricker contended that this rate may be taken as a maximum and supported this contention by the following arguments. On general grounds it seems likely that mortality should be greater while salmon are small than when they become larger. Intra- and inter-stock comparisons between size of smolts and total sea mortality demonstrate that larger smolts have greater survival (Ricker, 1962, fig. 1). His argument continues (p. 537), "We are particularly interested in the ocean mortality after the first ocean annulus is put down, after the sockeye are 25–35 cm long. The most straightforward estimate available is the average ocean natural mortality rate for the largest smolts available, which are the Karluk 3-freshwater type", and (p. 538) "It is likely, of course, that even the Karluk smolts experience a somewhat greater mortality rate during the early part of their ocean life than they do in the later part". Thus the bias of using $q = 0.038$ for ocean natural mortality rate is in the direction of being too great.

Fredin (MS, 1963) developed 4 population models representing different concepts of the distribution of natural mortality during the ocean life of sockeye. The first model dealt with a constant monthly instantaneous rate throughout ocean life. In the second model, the monthly instantaneous mortality rate decreased arithmetically during ocean residence. In the third model, the monthly instantaneous mortality rate decreased geometrically during the first 6 months of ocean life and remained constant thereafter. The fourth model dealt with a "catastrophic" age-specific first month instantaneous mortality rate and a constant mortality rate thereafter. Using Karluk sockeye data, values of g according to Model 1 were 0.045 for 2-freshwater and 0.039 for 3-freshwater annuli groups. Under Model 2, values of g fell from 0.056 to 0.059 for 2-freshwater and from 0.047 to 0.007 for 3-freshwater annuli groups. Under Model 3, values of g were 0.015 and 0.013 for the 2- and 3-freshwater annuli groups, respectively, after the first year in the sea. Under Model 4, $g = 0.023$ after the initial ocean year.

Taguchi (1961b) presented an ingenious model for estimating natural mortality rates between the time that sockeye in their ultimate year are found by the oceanic fishery and their arrival at the coast. His instantaneous rate M_0 is most nearly equivalent to $q + k$ of my notation. Taguchi estimated for sockeye that $M_0 + 0.690$ on a per month basis. From Parker (1962a) it is estimated that $q + k \simeq 0.035$. The former is nearly 20 times the latter estimate; in fact, if allowed to apply for two months, Taguchi's rate accounts for all of the total sea mortality observed in both the Karluk and Dalnee stocks.

Taguchi's estimate is based upon several rather critical assumptions. An integral part of his solution of M_0 is the estimate of $M_0 + M_1$ where M_1 is the additional mortality rate applicable to fish which encounter the nets and escape in the oceanic fishing area. $M_0 + M_1$ was estimated by use of 2-site tagging experiments. The 2 sets of data used are reproduced here as Table X. Taguchi's equation for depicting tag recovery is:

$$N_t = uN_0e^{-(M_0 + M_1)t} \tag{4}$$

where N_0 denotes the tagged population at time of release, N_t the recaptures after t days of freedom, and u the rate of exploitation. Two sets of data (a and b) were used as simultaneous equations leading to the equality

$$e^{-(M_0 - M_1)(t_a - t_b)} = \frac{N_{ta}\, N_{0b}\, u_b}{N_{tb}\, N_{0a}\, u_a} \tag{5}$$

Taguchi assumed no differences among the u's and that in the first set that t_b was so short that $t_b(M_0 + M_1) = 0$. Thus the data of Table X yielded the solutions

$$e^{-(M_0 + M_1)14} = \frac{(354)\ (19)}{(326)\ (36)} = 0.573$$

$$14(M_0 + M_1) = 0.557$$

$$M_0 + M_1 = 0.0398 \text{ (per day)}$$

and

$$e^{-(M_0 + M_1)19} = \frac{(265)\ (44)}{(506)\ (45)} = 0.512$$

$$19(M_0 + M_1) = 0.669$$

$$M_0 + M_1 = 0.0352 \text{ (per day)}$$

These values were next averaged and $M_0 + M_1 = 0.0375$ used in his model to obtain other estimates including M_0[10].

Equation (5) does not, however, adequately depict the survival of a tagged salmon population. Sources of mortality may be conveniently grouped into short- and long-term effects (Parker *et al.*, 1963) the former being complete within 1 or 2 days, the latter continue for life. A short-term effect cannot be calculated

[10]The above results differ slightly from Taguchi's as I have corrected minor arithmetic errors.

TABLE X. Sockeye tagging experiments used to estimate $M_0 + M_1$[a,b].

Tagging sites	Years of tagging	Number of fish: Tagged N_0	Number of fish: Recovered N_t	Average time at liberty t
Commander Island to Kamchatka Bay				
a) Pelagic drift nets	1938–39	326	19	14
b) Set nets, Kamchatka Bay	1935–37	354	36	2
North Kurile Island to Ozernaya River				
a) Off-shore drift nets	1938	506	44	21
b) Estuary of Ozernaya River	1931	265	45	2

[a]$M_0 + M_1$ denotes the instantaneous rate of natural mortality (M_0) and the additional instantaneous mortality rate caused by fish being caught but not retained by gill-nets (M_1) as used by Taguchi, 1961b.

[b]Data from Taguchi, 1961b, appendix 3.

as an instantaneous rate and then extrapolated in time. Long-term effects are of 2 types: (1) those that serve to intensify the effects of prevailing sources of mortality and (2) those which are independent of the prevailing natural mortality rate. Thus a minimum statement for recapture of tagged salmon would be

$$N_t = N_0(1 - M)\ u r a e^{-t(mq + j)} \tag{6}$$

Here N_t denotes the number of tags recovered

- N_0 the original tagged population
- u the rate of exploitation
- r the fraction of tagged fish recovered, recognized and reported
- a any increase in susceptibility to fishing caused by the tag
- M the immediate mortality rate from captive tagging and handling
- m the coefficient describing any increase in the intensity of natural mortality factors caused by the tag
- q the instantaneous natural mortality rate for unmarked fish
- j the instantaneous rate of tag loss (due to tag failure)

In a 2-site tagging experiment we might expect that u, r and a are equalities thus 2 sets of data (a and b) would lead to the equality

$$e^{-(t_a - t_b)(mq + j)} = \frac{(N_{1a})(N_{0b})(1 - M_{2b})}{(N_{1b})(N_{0a})(1 - M_{2a})} \tag{7}$$

The solution of equation (7) necessitates either the assumption that $M_a \equiv M_b$ or the independent evaluation of each parameter. The assumption of identity is implicit in Taguchi's treatment for M_2 is included in u. Studies reported by Parker *et al.* (1959) have shown large differences between short-term mortalities depending upon the physiological stage of the fish involved. Coho (*O. kisutch*), taken by troll gear off the coast of Alaska during July and August of their ultimate year, were feeding voraciously and were relatively immature. After selection against

serious injury short-term mortality was estimated at approximately 44% (within the 95% confidence interval of 34% and 52%), mainly occurring after the first hour but prior to the sixth hour following capture. On the other hand maturing non-feeding coho taken in September and similarly treated in the lower reaches of the Taku River, Alaska, all survived and were released after 24–50 hours. If these fish were to be used for a 2-site tagging experiment the ratio

$$\frac{1 - M_{2b}}{1 - M_{2a}} = \frac{1.00}{0.56} = 1.786$$

would need to be employed in the equation. Admittedly this experiment may represent a more extreme situation than Taguchi's. Unfortunately, similar experiments have not been carried out with sockeye, and this constitutes a serious deficit in the interpretation of data from tagging. Likewise the marking (or tagging) coefficient m has not been defined for tagged sockeye salmon. Recalling that Taguchi's solutions for $e^{-t(M_0 + M_1)}$ produced survivals of 0.573 and 0.512, the equivalent mortalities, 42.7% and 48.7%, are well within the 0.95 confidence interval for immediate mortality of tagged coho. I contend that Taguchi has not demonstrated the existence of any natural mortality whatever for the mortality that has been demonstrated may reasonably be ascribed to the effects of tagging on the basis of present knowledge.

EFFECT ON YIELD

From the foregoing arguments estimates of growth and mortality rates have been computed which allow a decision as to whether the sockeye stocks are gaining or losing weight during their penultimate and ultimate years in the sea. From data provided by INPFC for 1961 (Statistical Year Book, 1961) and from the tagging experiments of FRI already cited, western Alaska sockeye are apparently taken by the pelagic fishery about 20–30 days prior to their arrival at the coast. Taguchi (1961b) estimates that western Kamchatka sockeye are, on the average, taken by the pelagic fishery about 55 days prior to their arrival on the Kamchatkan coast. It is permissible to state as a conservative estimate then that sockeye taken by the pelagic fishery while in their ultimate year have the capability of growing for at least 30 additional days. During this period the mortality rate is estimated as $q + k = 0.035$.

Sockeye taken by the pelagic fishery while in their penultimate year would have a potential of approximately 8 months growth during that year and approximately 5 months growth during the ultimate year. Mortality during this period is estimated as 12 months at the rate $q = 0.026$ and one month at $q + k = 0.035$. These values are combined in the first 6 columns of Table XI to estimate the potential change in stock mass during the time periods in question. It is obvious at this point (Table XI, col. 6) that regardless of the proportions of fish of the various life history types there is an expectation of a net gain in biomass in the ensuing pelagic and migratory phases of life.

The percentages of the fishable stock (45 cm fork length and over) that are in the ultimate and pre-ultimate years are important to the present problem.

TABLE XI. Estimating potential changes in mass of pelagic catches of sockeye.

Life history type	Time in months (t)	Instantaneous rates of change: growth (g)	mortality (q)	mortality ($q + k$)	mass $[g - (q + k)]t$	Weighting factors
2-ocean annuli						
Ultimate year	1	0.111		0.035	0.076	0.410
3-ocean annuli						
Penultimate year	8	0.059	0.026		0.264	0.143
Ultimate year	4	0.075	0.026		0.196	
Ultimate year	1	0.075		0.035	0.040	0.446

Potential change in mass of fish caught pelagically if they were allowed to reach the coast and the survivors captured there:

$$\underbrace{0.410e^{0.076}}_{\text{2-ocean annuli fish in ultimate year}} + \underbrace{0.446e^{0.040}}_{\text{3-ocean annuli}} + \underbrace{0.143e^{8(0.059-0.026)+4(0.075-0.026)+0.040}}_{\text{3-ocean annuli fish in penultimate year}} = 1.142$$

These statistics have not been encountered in the literature, however it is possible to estimate them for the important Asian and North American stocks by using age of return data and the oceanic mortality rate $q = 0.026$. Royce *et al.* (1962, table 10) present estimates of returns of western Alaska sockeye by ocean ages for the years 1956 to 1960. Totalling the contribution of each ocean age the return of 2-ocean annuli type was 84.5 million and 3 or more ocean annuli type was 46.7 million fish. It is assumed that these data for 6 years are representative of the average proportion of western Alaska sockeye which mature after 2 or 3 winters at sea. Prior to the separation of the maturing group from the immature remainders the fishable stock consists principally of ultimate year 2- and 3-ocean annuli and penultimate year 3-ocean annuli type fish. Thus

$$84.5 + 46.7 + 46.7e^{12(0.026)} = 195.0$$

of which $46.7e^{12(0.026)} = 63.8$ are not in their ultimate year. The average percentage of the fishable stock of pre-ultimate age is $63.8/195.0 = 32.7\%$.

Hanamura (1961, table 6) presents age data for Kamchatka River sockeye for the return years 1957–1960. For these 4 years the escapement, on the average, consisted of 8.6% 2-ocean, 83.4% 3-ocean and 8.0% 4-ocean annuli fish. The relative proportions of fish, in respect to year of return, consisting of the fishable stock in the ocean habitat prior to the shoreward departure of the maturing group are:

$$8.6 + 83.4 + 8.0 = 100.0 \text{ ultimate year fish}$$
$$(83.4 + 8.0)e^{12(0.026)} = 124.9 \text{ penultimate year fish}$$
$$\text{and } 8.0e^{24(0.026)} = 14.9 \text{ antepenultimate year fish.}$$

The estimated percentage of pre-ultimate year fish is 58.3%.

From Hanamura (1961, table 8.2) the average ocean age of returning Kurile sockeye based on many years (1940 to 1955) is calculated as 31.2 2-ocean, 67.8 3-ocean, these accounting for 99% of the total. From these data it is estimated that 48.3% of the fishable stock, prior to the shoreward migration of the maturing component, is in the pre-ultimate years.

The actual percentage of the fishable stock present at any specific time that is not maturing depends upon several fluctuating factors such as the relative contributions of stocks, brood years and the timing of the departures of maturing components. From the information developed above, this percentage may be as low as 33% if only Western Alaska fish are present and 58% if a pure Kamchatka River stock is fished prior to the shoreward migration. After the maturing component begins its shoreward migration this percentage increases to approach 100%. Data are not sufficient with which to more accurately describe the dynamics of this statistic.

Yamanaka (1963, table 1) presents catch statistics of the pelagic fisheries in the northwestern Pacific for the years 1957–1959, by which the percentage of non-maturing fish for these years may be calculated. During 1957, 6.2% of the total number of sockeye taken were non-maturing. In 1958, 15.1% and in 1959 31.2% of the catch were non-maturing. Essentially the same estimates are given by Hanamura (1961, table 24.2). Evidently this statistic is quite variable and in addition to factors given above which affect the proportion of the fishable stock which is of pre-ultimate age, the proportion of pre-ultimate age fish entering the catch also depends upon spatial distribution and gear selectivity relative to the maturing and non-maturing components of the population.

To provide a realistic example of the effects of pelagic fishing on yield, the catches of the Japanese pelagic fishery during the years 1957–1959 will serve as a basis. During this period catches totalling 41,398,000 fish contained 5,925,000 individuals considered to be of pre-ultimate age (Yamanaka, 1963, table 1). Thus 14.3% of the number caught may be termed non-maturing and 85.7% may be termed maturing. The proportions of this catch which belonged to North American and Asian stocks is not known but are assumed, for this example, to be equal. To arrive at a division of the mature component into ocean age types, a simple average of Western Alaska and Kuril stocks will suffice, thus for 2-ocean annulus,

$$[(64.4\% + 31.5\%)/2]\ 85.7\% = 41.0\%.$$

For the 3-ocean annulus types,

$$[(35.6\% + 68.5\%)/2]\ 85.7\% = 44.6\%.$$

These percentages serve as weights in the yield calculations set forth in Table XI.

These calculations lead to two conclusions: (a) the instantaneous growth rate exceeds that of natural mortality resulting in a positive increment to the mass of the stock during both the penultimate and ultimate years; (b) the positive growth potential is far from insignificant; it amounts to 14.2% in the example used, which is deliberately conservative.

DISCUSSION

From the foregoing arguments it is evident that, for the important growth types of both Asiatic and North American sockeye, fishing should be restricted to coastal waters as close as possible to the estuaries of natal streams, if maximum yield from the stocks is seriously desired. Ricker (1962) and Fredin (MS, 1963) came to essentially the same conclusions for the stocks which they studied. On the other hand, Taguchi (1961b) concluded that pelagic fishing was the more rational, that natural mortality was so high that a reduction in the stock mass took place during the migration from oceanic to coastal waters in the ultimate year and therefore fishing should be carried out on the high seas. Taguchi's model and the treatment of his data have already been discussed and found to be unacceptable (page 1385).

Yamanaka (1963) considers the effects of prohibiting the catching of sockeye in their penultimate year on the yield of the stock to the pelagic fishery. In his model, the instantaneous rate of fishing, F, is assumed to be constant under either condition of fishing or non-fishing of the pre-ultimate age portion of the stock, hence part of the possible catch of immatures would eventually escape the fishery as matures and migrate to the coast. Under these conditions, the growth rate must compensate for the additional escapement as well as natural mortality in order to equalize the yields possible under either alternative.

It is not clear how Yamanaka arrived at his growth coefficients. Presumably these were derived as simple quotients of the ultimate year average weight divided by the pre-ultimate age average weight of pelagic fishing catches. The selective action of the gillnets upon the pre-ultimate age component would certainly lead to a serious underestimation of growth.

Values of F and q were borrowed from Taguchi (1961b) and, with these data and rates, Yamanaka concluded that a slight advantage in yield to the pelagic fishery is possible by fishing for immatures. Yamanaka's model does not fairly represent the situation under discussion because the assumption of constant F is not a realistic requirement of all salmon fisheries. In theory and, in many cases, in practice, escapements to the spawning grounds can be adjusted by simple manipulation of fisheries operating in the coastal regions close to the parent streams. Indeed Ricker (1958) describes the properties of models where management is geared to optimum escapement and indicates the gain achieved thereby in terms of reproduction and yield. Shepard and Withler (1958) recommended this type of management on the Skeena River, British Columbia.

The yield problem has received study in respect to other members of the genus *Oncorhynchus*. Taguchi (1961c) came to the same conclusions for Asian chum salmon (*O. keta*) as for sockeye, using the same model and techniques. Doi (1962) has considered chum salmon as an example in a theoretical population model. Like that of Yamanaka, Doi's model postulates a constant rate of exploitation, thus growth increments must exceed not only losses from natural mortality but for the additional escapement arising from reducing the fishing time from two years to one. It is obviously more appropriate to consider the

needs for reproduction first and then gain the maximum yield from the allowable catch. Parker (1959) studied the relationships between natural mortality and growth for chinook salmon and concluded that maximum yield could only be obtained by fishing the maturing population close to the estuaries of natal streams.

It is evident, however, that the available data pertaining to growth and natural mortality rates are insufficient to allow an entirely conclusive argument on at what time, precisely, fishing should take place in the final stages of life history in the sea. It is of particular interest to evaluate mortality rates for short intervals of time during this period. Likewise, while it is generally known that growth slows and finally ceases as sockeye approach the estuary and enter fresh water, the details have not been studied. In the meantime, we can only conclude that, in general, yield from sockeye stocks of the North Pacific is depressed by a pelagic fishery.

ACKNOWLEDGMENTS

Drs P. A. Larkin and W. E. Ricker and Mr F. C. Withler of the Fisheries Research Board of Canada Biological Station at Nanaimo, and Messrs R. A. Fredin and R. Lander of the U.S. Bureau of Commercial Fisheries, Biological Laboratory at Seattle were very helpful with their suggestions and criticisms of the manuscript.

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APPENDIX A

Recovered during year of tagging, 121 fish. Fisheries Research Institute North Pacific sockeye tagging.

Tag No.	Date		Length	
	Tagged	Recovered	At tagging	At recovery
12520	19 June 57	23 June 57	580	605
34270	14 June 57	9 June 57	545	560
32806	13 June 57	20 June 57	570	595
42441	12 June 57	19 June 57	575	595
6498	6 June 57	24 June 57	535	565
124056	6 June 57	21 June 57	570	595
32419	6 June 57	15 June 57	535	555
32460	6 June 57	13 June 57	565	577
124077	6 June 57	23 June 57	555	560
6646	6 June 57	17 June 57	495	510
6477	6 June 57	22 June 57	550	560
32398	6 June 57	20 June 57	545	560
6713	6 June 57	25 June 57	520	530
8414	29 May 58	19 June 58	585	630
8903	13 June 58	20 June 58	565	580
C-150	18 July 58	8 August 58	500	510
20939	18 July 58	8 August 58	505	520
L-470	20 July 58	9 August 58	535	540
8758	27 June 58	7 August 58	480	500
P-004	27 May 59	30 June 59	560	580
7382	15 July 60	29 July 60	485	520
P-641	18 May 60	8 June 60	495	520
P-653	18 May 60	24 July 60	500	550
P-740	18 May 60	16 July 60	480	520
P-873	30 May 60	17 June 60	530	550
P-892	30 May 60	15 June 60	550	620
P-946	30 May 60	2 June 60	485	500
P-976	30 May 60	20 June 60	450	480
P-982	31 May 60	18 June 60	535	560
Q-010	31 May 60	19 June 60	500	520
Q-020	31 May 60	15 June 60	605	(550)
Q-059	31 May 60	18 June 60	515	550
5125	14 June 60	20 June 60	325	470
5161	16 June 60	21 June 60	510	(500)
5162	16 June 60	20 June 60	485	500
5164	16 June 60	19 June 60	505	520
5169	16 June 60	22 June 60	545	550
5186	16 June 60	23 June 60	535	540
5192	16 June 60	23 June 60	485	500
5203	16 June 60	23 June 60	500	500
5210	16 June 60	22 June 60	575	(520)
Q-195	1 June 60	9 June 60	495	510
Q-242	1 June 60	21 June 60	475	480
Q-317	1 June 60	12 June 60	535	550
4125	5 June 60	17 June 60	560	(540)

Appendix A (continued)

Tag No.	Date		Length	
	Tagged	Recovered	At tagging	At recovery
Q-462	6 June 60	18 June 60	500	530
Q-463	6 June 60	22 June 60	540	540
Q-472	6 June 60	15 June 60	590	600
Q-479	6 June 60	20 June 60	555	570
Q-489	6 June 60	18 June 60	525	540
Q-498	6 June 60	19 June 60	520	540
Q-504	6 June 60	21 June 60	470	485
4177	6 June 60	22 June 60	540	545
4192	6 June 60	12 June 60	560	575
4249	6 June 60	11 June 60	505	530
4252	6 June 60	22 June 60	500	560
4258	6 June 60	22 June 60	540	550
4265	6 June 60	20 June 60	530	550
4354	6 June 60	16 June 60	515	540
4395	6 June 60	22 June 60	510	510
4419	6 June 60	21 June 60	485	500
4468	7 June 60	19 June 60	500	515
4479	7 June 60	18 June 60	495	510
4491	7 June 60	17 June 60	480	480
4545	7 June 60	27 June 60	505	(490)
4589	10 June 60	14 June 60	545	570
4613	10 June 60	22 June 60	520	540
4645	10 June 60	20 June 60	545	550
4664	10 June 60	22 June 60	485	500
4665	10 June 60	18 June 60	495	510
4681	10 June 60	24 June 60	495	565
4713	10 June 60	20 June 60	525	550
4768	10 June 60	22 June 60	540	540
4782	10 June 60	19 June 60	535	550
4814	10 June 60	17 June 60	510	540
4854	10 June 60	15 June 60	510	530
4883	10 June 60	18 June 60	500	500
4901	10 June 60	17 June 60	500	510
4902	10 June 60	22 June 60	540	560
4939	10 June 60	18 June 60	485	485
5496	20 June 60	28 July 60	500	520
G-918	10 July 60	29 July 60	475	(470)
Q-539	7 June 60	20 June 60	515	550
Q-542	7 June 60	19 June 60	525	545
Q-572	7 June 60	22 June 60	510	530
Q-584	7 June 60	27 June 60	490	490
Q-596	7 June 60	18 June 60	485	500
Q-597	7 June 60	17 June 60	530	540
Q-607	7 June 60	1 July 60	580	596
Q-629	7 June 60	21 June 60	480	510
Q-638	7 June 60	18 June 60	545	570
Q-659	7 June 60	16 June 60	555	590
13024	7 June 61	17 June 61	570	580

Appendix A (continued)

Tag No.	Date		Length	
	Tagged	Recovered	At tagging	At recovery
13026	7 June 61	13 June 61	555	(550)
13049	7 June 61	8 June 61	645	650
13024	7 June 61	17 June 61	570	580
13026	7 June 61	13 June 61	555	580
13049	7 June 61	8 June 61	645	650
13056	7 June 61	15 June 61	585	645
13083	7 June 61	10 June 61	565	570
13151	7 June 61	10 June 61	620	620
13158	7 June 61	16 June 61	545	560
13166	7 June 61	14 June 61	610	620
13174	7 June 61	17 June 61	530	550
13178	7 June 61	17 June 61	630	(540)
13212	7 June 61	17 June 61	560	570
13240	11 June 61	16 June 61	645	660
13246	11 June 61	18 June 61	520	530
13253	11 June 61	17 June 61	450	460
13325	11 June 61	16 June 61	505	(490)
13382	11 June 61	13 June 61	575	580
13439	11 June 61	16 June 61	570	590
13443	11 June 61	16 June 61	560	580
13554	11 June 61	17 June 61	545	560
13574	11 June 61	18 June 61	575	590
13580	11 June 61	16 June 61	615	(540)
13631	11 June 61	18 June 61	545	570
13672	11 June 61	17 June 61	510	530
13758	11 June 61	13 June 61	590	600
13765	11 June 61	17 June 61	495	505
13772	11 June 61	16 June 61	520	520

APPENDIX B

Recovered in year after tagging, 57 fish. Fisheries Research Institute North Pacific sockeye tagging.

Tag No.	Date		Length	
	Tagged	Recovered	At tagging	At recovery
16589	9 August 56	20 July 57	470	580
16825	11 August 56	3 June 57	460	549
16321	3 August 56	24 June 57	505	582
13300	2 August 56	25 May 57	495	580
17200	3 August 56	12 June 57	475	610
13852	15 August 56	22 June 57	465	560
17005	2 August 56	13 June 57	495	580
16867	11 August 56	15 June 57	475	570
13071	13 August 56	24 June 57	420	530

Appendix B (continued)

Tag No.	Date		Length	
	Tagged	Recovered	At tagging	At recovery
13881	15 August 56	31 May 57	500	580
13355	2 August 56	6 July 57	500	530
16935	11 August 56	7 July 57	450	575
44254	15 August 57	20 May 58	460	560
C-393	18 July 58	16 May 59	490	542
E-988	14 July 58	27 June 59	315	490
L-446	20 July 58	14 June 59	390	500
L-445	20 July 58	28 June 59	375	483
C-405	18 July 58	16 July 59	450	610
28044	13 August 58	14 July 59	360	470
9567	30 June 58	15 June 59	475	560
28012	13 August 58	3 June 59	440	540
19927	15 August 58	27 June 59	465	550
46935	30 August 59	15 June 60	470	560
30824	23 July 59	16 June 60	335	540
06832	10 July 60	4 June 61	485	560
06850	10 July 60	6 June 61	445	520
06891	10 July 60	6 July 61	465	580
06937	10 July 60	22 June 61	475	590
46884	9 July 60	15 June 61	410	540
46891	9 July 60	17 June 61	420	590
46979	9 July 60	18 June 61	430	550
G-00593	9 July 60	13 June 61	440	560
G-00733	9 July 60	5 June 61	445	550
G-00877	9 July 60	7 June 61	435	540
G-00892	9 July 60	12 June 61	430	590
47693	10 July 60	13 June 61	425	540
47719	10 July 60	16 June 61	450	570
47720	10 July 60	8 June 61	425	572
47763	10 July 60	18 June 61	435	565
J-00296	15 July 60	18 June 61	445	540
J-00311	15 July 60	9 June 61	475	600
02721	29 June 60	9 June 61	455	610
03429	2 July 60	9 June 61	470	590
D-00281	4 July 60	14 June 61	470	550
M-00369	4 July 60	17 June 61	455	580
D-00657	6 July 60	11 June 61	485	600
23892	16 August 61	16 June 62	385	480
19005	16 August 61	27 June 62	450	544
19027	16 August 61	1 June 62	395	530
19041	16 August 61	3 June 62	480	580
19086	16 August 61	4 July 62	480	570
22869	20 July 61	16 June 62	380	493
23081	21 July 61	3 July 62	370	490
23216	21 July 61	13 July 62	365	470
23108	22 July 61	2 July 62	380	420
23116	22 July 61	7 July 62	370	450
23331	22 July 61	2 June 62	380	500

Studies on the Life History and Ecology of the Bigmouth Buffalo, *Ictiobus cyprinellus* (Valenciennes)[1,2]

By R. P. Johnson

Saskatchewan Fisheries Laboratory
Saskatoon, Saskatchewan

ABSTRACT

The field study of the bigmouth buffalo (*Ictiobus cyprinellus* (Valenciennes)), conducted mainly in 1955 and 1956, was concentrated on two small eutrophic lakes in the Qu'Appelle River drainage of Saskatchewan. The bigmouth buffalo reaches its northern limit of range in the Qu'Appelle drainage. Migration into Saskatchewan was probably through postglacial connections at the headwaters of the Mississippi and Red River systems. In the lakes studied, the species prefers water shallower than 5 m.

The relation of standard length to fork length and of fork length to weight is presented graphically, and the latter described by the equation: weight in pounds = (0.00097 fork length in inches)$^{2.91}$. Length–frequency distributions and age determinations from scale reading show that the population studied was largely the very successful 1948 year-class, produced in a year of extensive flooding. Annulus formation occurred during the second or third week in June. Growth of the 1948 year-class in Pasqua Lake was extremely slow, probably influenced by the cool climate and population density here.

Food of young buffaloes was mainly Cladocera and Copepoda. Larger buffaloes ate about 75% Entomostraca and 15% chironomids, the latter more important as the size of fish increased. Analysis of the living habits of the food eaten, and the feeding mechanism of the buffalo, shows that they occupy a food niche overlapping both bottom feeders and limnetic plankton feeders.

Sexual maturation, especially of females, was extremely slow both in age and size as compared with southern populations. Examination of gonads suggests spawning occurs about May 18–25. Egg measurements indicate that females do not all spawn each year. The contention by other investigators that spawning is "triggered" by addition of fresh water analogous to normal spring floods of the Mississippi River is supported by the present study.

The population in the Qu'Appelle drainage is probably dependent on the very sporadic production of strong year-classes. A more stable population would require association with regular spring floods of a nearby river or marsh. Commercial removal from the viewpoint of greatest productivity is most economical at the smallest marketable size, as yearly weight gains are probably more than offset by natural mortality.

INTRODUCTION

The bigmouth buffalo is the only catostomid of the genus *Ictiobus* occurring in Saskatchewan. At present it supports a small and erratic commercial fishery in this province, but for many years has been an important commercial species in the Mississippi system. In Saskatchewan the species is regarded as a rough fish, and accused of detrimental effects on game fish populations. A life-history study is desirable to provide information on its relation to other species of fish,

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and its value as a commercial fish. In recent years the bigmouth buffalo has been the object of revived interest in pond culture in the United States (Swingle, 1949, 1954, 1957). In the future such a source of protein food may have unpredicted importance even in agricultural Saskatchewan.

Basic lake surveys have been carried out on several Saskatchewan lakes in which buffaloes occur. During these surveys gill nets and seines captured few buffaloes, although they were known to be abundant. The present investigation, carried out from 1955 to 1958, seeks to understand the ecology and to summarize available information concerning this species.

METHODS

Fish populations in 1955 and 1956 were sampled by means of gill nets and seines. Gill nets used were of sizes 3-, 4-, 5-, 5½-, and 7-inch stretched mesh (76, 102, 127, 140 and 178 mm). Each net was left as nearly as possible for 24 hr per set. Two seines were used to capture fish, one 30 ft (9.2 m) and the other 90 ft (27 m) long, both about 6 ft (1.8 m) deep, and of ½-inch (13-mm) stretched mesh. Through the kindness of Mr J. Harwood many length measurements of buffaloes held in a commercial fishery trap were made in August 1956, and a few samples were obtained at other times. Very small fish were captured with a metal kitchen sieve. Distribution records and samples of buffaloes obtained by lake and stream surveys from 1951 to 1958 have been used where available.

The life history stages described follow Lagler (1956). "Young" refers to young-of-the-year fish, or members of age-group 0. "Juveniles" are those fish older than age-group 0 but not yet mature, while "adults" are mature fish.

Samples of young buffaloes were preserved in 10% formalin; larger fish were examined in the field. Since buffaloes do not have a distinct stomach, the contents of the intestine of larger specimens were preserved for later examination. Sex, maturity, and condition of the gonads were recorded and some gonads preserved.

Scale samples were taken from the left side of the fish, midway between the origin of the dorsal fin and the lateral line. Age determinations were made by interpreting annuli on plastic impressions of the scales. Scales too large to be accommodated in a conventional microprojector were examined with a stereomicroscope.

Laboratory analysis of intestinal contents was made by examination under a binocular microscope. The percentage by volume of each food item was estimated.

The size of buffalo eggs was measured with an ocular micrometer. Estimation of the number of eggs in an ovary was made by counting the eggs in a small volume of the ovary, determining the volume of the ovary, and calculating by proportion the number of eggs. This method is essentially the same as described by Stone (1937), who found an average error of 5.1% when comparing estimated and actual numbers of eggs in 9 cisco ovaries.

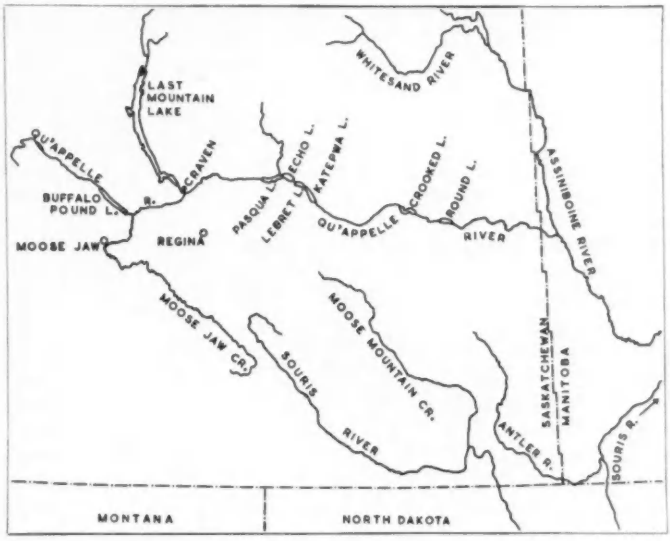

FIG. 1. Map of southeastern Saskatchewan showing major features of the Qu'Appelle River.

STUDY AREAS

Echo and Pasqua Lakes were the areas chosen for intensive study of the bigmouth buffalo. This choice was influenced partly by the commercial buffalo fishery which exists on Pasqua Lake, and partly for expediency in transportation and accommodation. These lakes, situated about 50 miles (80 km) east and north of Regina (Fig. 1), are two of a series formed by depressions in the watercourse of the Qu'Appelle River.

A summary of the morphometry of each lake is as follows:

	Pasqua	*Echo*
Area, *miles*² (*km*²)	5.4 (14)	4.5 (11.7)
Length, *miles* (*km*)	7.4 (11.9)	4.2 (6.8)
Maximum width, *miles* (*km*)	1.2 (1.9)	1.0 (1.6)
Maximum depth, *m*	15.5	22.0
Mean depth, *m*	7.2	10.4
Percentage of area in 0–5 *m* depth zone	40	30

Both lakes are highly eutrophic, with heavy standing crops of bottom fauna and plankton. Dense blue-green algal blooms occur frequently. Thermal conditions in different years range from almost complete mixing throughout the summer, to development of a pronounced thermocline which persists throughout the summer.

TABLE I. List of fishes collected in Pasqua and Echo Lakes, with estimates on the relative abundance of each kind. Nomenclature follows that of the American Fisheries Society (1960).

Species	Relative abundance
Cisco, *Coregonus* sp.	abundant
Lake whitefish, *Coregonus clupeaformis* (Mitchill)	common
Northern pike, *Esox lucius* Linnaeus	common
Carp, *Cyprinus carpio* Linnaeus	rare
Emerald shiner, *Notropis atherinoides* Rafinesque	abundant
Spottail shiner, *Notropis hudsonius* (Clinton)	abundant
Fathead minnow, *Pimephales promelas* Rafinesque	common
Quillback, *Carpiodes cyprinus* (LeSueur)	rare
White sucker, *Catostomus commersoni* (Lacépède)	abundant
Bigmouth buffalo, *Ictiobus cyprinellus* (Valenciennes)	abundant
Northern redhorse, *Moxostoma macrolepidotum* (LeSueur)	rare
Black bullhead, *Ictalurus melas* (Rafinesque)	rare
Burbot, *Lota lota* (Linnaeus)	common
Brook stickleback, *Eucalia inconstans* (Kirtland)	rare
Ninespine stickleback, *Pungitius pungitius* (Linnaeus)	abundant
Trout-perch, *Percopsis omiscomaycus* (Walbaum)	rare
Iowa darter, *Etheostoma exile* (Girard)	common
Johnny darter, *Etheostoma nigrum* Rafinesque	rare
Yellow perch, *Perca flavescens* (Mitchill)	abundant
Walleye, *Stizostedion vitreum vitreum* (Mitchill)	common

There are at least 20 species of fishes present in Pasqua and Echo Lakes. These are listed in Table I, with information on relative abundance. The estimates of abundance are based on netting and seining during 5 years of study on the lakes.

Scale samples and ecological information from Buffalo Pound, Last Mountain, Katepwa, Crooked, and Round Lakes, and the Qu'Appelle River have been used where pertinent (Fig. 1).

DISTRIBUTION

GEOGRAPHIC DISTRIBUTION

Figure 2 shows the distribution of the bigmouth buffalo in North America. The literature listed in Distribution References was used in the preparation of the map, in addition to pertinent text references. Records based on personal communications are credited in the text.

The bigmouth buffalo is widespread through the Mississippi River basin. In the northwestern Missouri River drainage it is reported by Mr William Alvord (personal communication) as common in Fort Peck Reservoir and present in a small lake of the Milk River drainage near Malta, Montana. In North Dakota it is found in and below the Garrison Reservoir on the Missouri River.

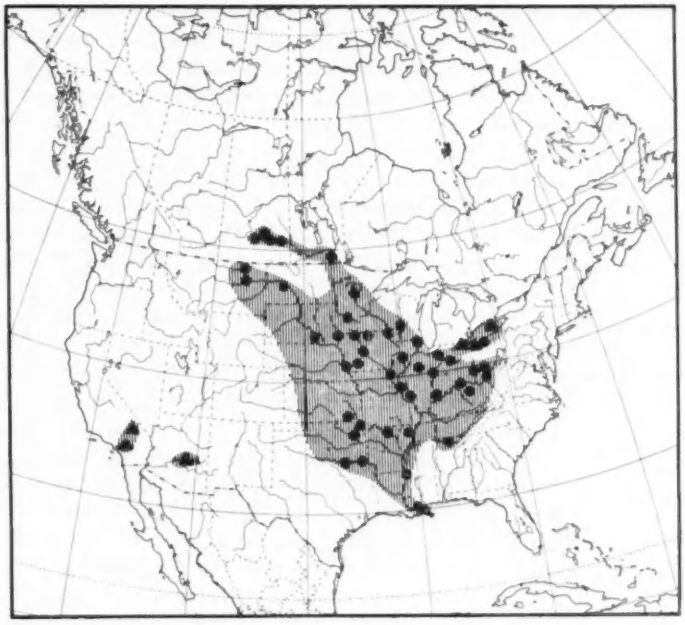

FIG. 2. Distribution of the bigmouth buffalo, *Ictiobus cyprinellus*. Circles show natural occurrence and triangles show introductions.

Ictiobus cyprinellus ranges into Texas in the Mississippi drainage system, but is relatively rare (Knapp 1953). It is not reported from the Gulf of Mexico drainages east of the Mississippi River, but it occurs in the Gila River drainage in Arizona. This is considered to be the result of introduction (Dr R. M. Bailey, personal communication). Moore (1957) wrote that it is "well established in some Arizona impoundments". Introductions have also been made into the Los Angeles aqueduct system in California (Evans, 1950).

The only drainage system of the Atlantic slope occupied by the bigmouth buffalo is the Great Lakes system, and here it occurs only in Lake Erie and its tributaries. Native occurrence here has been discussed by Hubbs (1930). Remarking on a specimen collected by Kirtland at Rockport, Ohio, in 1854, Hubbs wrote ". . . this species has at least sporadically occupied the Lake Erie watershed for many years". Trautman (1957) reported stocking of buffaloes in western Lake Erie in 1920, and gave references of captures in later years. Recently, Scott (1957) listed a specimen from the Ontario side of Lake Erie at Long Point Bay.

Bigmouth buffaloes have been reported by Eigenmann (1895) from the "Red River of the North", and by Hinks (1943) from "Southern Manitoba". Mr B. Kooyman (personal communication) stated that recent extensive collecting throughout the southern part of Manitoba has turned up no specimens.

In Saskatchewan, the species is abundant in the 8 larger lakes of the Qu'Appelle drainage (see Fig. 1). Juveniles and adults have been captured in the Qu'Appelle River and Long Lake Creek near Craven, and young have been collected at various locations along the Qu'Appelle River from Craven to Pasqua Lake. Although it appears possible that the buffalo could be in the Frenchman, Souris, and Assiniboine River drainages in Saskatchewan, extensive seining has failed to disclose its presence.

It has been rumored that buffaloes were accidentally introduced into the Qu'Appelle drainage with a planting of bass in the first part of this century. They had received official notice, however, as early as 1887. Fishery Overseer F. C. Gilchrist (1888) wrote that buffaloes were common to all lakes of the Qu'Appelle Valley, and grow to 40 lb (18 kg) or more. He referred to them as *Ictiobus Bubalus*.

It is quite possible that buffaloes migrated into the Qu'Appelle River system. The headwaters of the Mississippi and Red River systems are near Big Stone Lake and Lake Traverse, on the South Dakota–Minnesota border. These two drainage systems were apparently connected during late glacial times, and even today the divide between them is not complete and the headwaters may merge during spring floods (Underhill, 1957). A more recent example of migration over the same route is that of the carp (Atton, 1959).

The original postglacial range of the bigmouth buffalo included the Mississippi River system, with some migration into other watersheds. Migration into the Great Lakes has been augmented by artificial introductions in recent years. The presence of buffaloes in Arizona and California drainages is apparently the result of introductions. Movement into the Red and Assiniboine parts of the Nelson River system occurred naturally, and although range extensions here have not been great, the buffalo is well established in the lakes of the Qu'Appelle Valley.

Habitat Distribution

Buffaloes prefer slow, sluggish, or still water and are typically inhabitants of larger rivers, oxbow and flood plain lakes and sloughs, bayous, and shallow lakes (Gerking, 1945; Eddy and Surber, 1947; Hubbs and Lagler, 1949; Moore, 1957; Trautman, 1957). O'Donnell (1935) found them abundant in all larger streams and flood plain lakes and present in small slow streams having drainage areas exceeding 300 square miles (780 km^2) in Illinois. Dr R. M. Bailey (personal communication) considers that, in the Mississippi Valley, they occur in waters of low gradient and moderate or slow current, not penetrating into waters of steep gradient.

The buffalo is well adapted to reservoirs, from which it is often reported. Trautman (1957) wrote that it appeared to be very tolerant of turbid water, and seemingly was a direct competitor with an associated species, the carp.

In the Qu'Appelle drainage, buffaloes are found mainly in the larger lakes. They readily invade marshes and backwaters during periods of spring flooding. Captures have been made in the spring by trap-net in Long Lake Creek and the Qu'Appelle River near Craven, and by seines and poison below Katepwa Lake

dam and Craven dam. Presumably their occurrence in these locations is concerned with spawning movements. They are reported to crowd into tributary streams and flooded marshes (Jordan and Evermann, 1937) and even shallow ditches (Trautman, 1957) during spring spawning.

Absence of buffaloes in the Frenchman and Souris Rivers may be due partly to intermittent flow of these streams, and partly to relatively steep gradients, since both are headwater streams. The Assiniboine River, however, while fluctuating greatly in volume, is never without runoff; the absence or rare occurrence of buffalo here is probably controlled by some other ecological factor, such as the absence of lakes.

Depth Distribution

Saskatchewan lakes in which buffaloes occur have maximum depths varying from about 5 m (Buffalo Pound Lake) to 30 m (Last Mountain Lake). Information from gill-netting indicates that the species prefers shallow water in all these lakes.

The depths at which buffaloes were caught in standard gang gill nets from 1951 to 1956 appears in Table II. They prefer water shallower than 5 m, although some catches were made in the 5- to 10-m depth zone in Crooked Lake.

Other gill-net catches made in 1955 and 1956 verify the shallow water preference of this species (Table III). In the 0- to 5-m zone the average catch

Table II. Total number of bigmouth buffaloes caught at different depths in standard gang gill nets. A standard gang net consists of 50-yard (46-m) lengths each of 1½-, 2-, 3-, 4-, 5-, and 5½-inch stretched mesh, each section about 6 ft or 1.8 m deep (numbers of sets in parentheses).

Depth zone	Pasqua 1955	Echo 1955	Crooked 1954	Crooked 1956	Round 1954	Last Mountain 1951
m						
0–5	16(4)	23(5)	1(5)	93(12)	1(7)	11(6)
5–10	0(3)	0(5)	0(6)	8(18)	0(8)	0(8)
10–15	0(4)	0(5)	0(5)	0(7)	0(6)	0(11)
15–20	...	0(5)	0(4)	0(7)	...	0(2)
20–25	...	...	...	...	...	0(5)
25+	...	...	...	...	...	0(2)

Table III. Average number of bigmouth buffaloes caught per 100 yards (91 m) of net of two meshes, set at different depths in Pasqua and Echo Lakes in 1955 and 1956 (numbers of sets in parentheses).

Depth	Pasqua 5-inch	Pasqua 7-inch	Echo 5-inch	Echo 7-inch
m				
0–5	29.5(21)	2.4(35)	52.6(17)	3.4(20)
5–10	2.3(4)	0.3(6)	2.0(2)	0.5(2)
10–15	0 (1)	...	...	0 (1)

per net set is from 7 to 25 times as great as in the 5- to 10-m zone. The greatest depth at which buffaloes were caught was 8.5 m.

GROWTH AND AGE DETERMINATIONS

Relation of Standard Length to Fork Length

Fork length measurements were used routinely, and all lengths given without qualification are in this unit. To facilitate comparison with standard lengths (Hubbs and Lagler, 1949), both measurements were made on 359 buffaloes from Pasqua and Echo Lakes in 1955 and 1956. The resulting relationship is seen in Fig. 3.

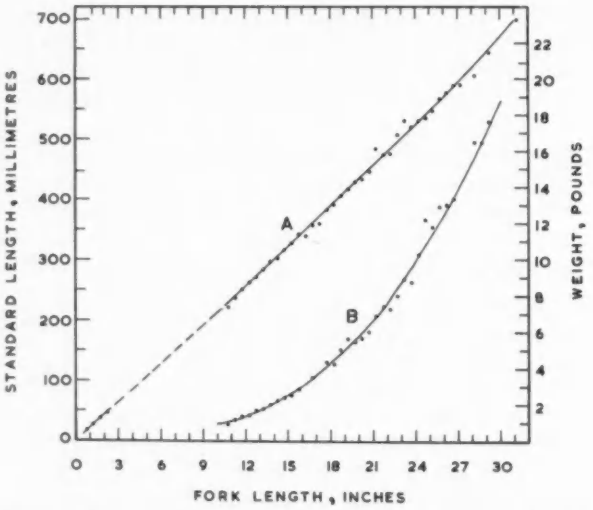

FIG. 3. Curve A — relationship of standard length to fork length for 359 bignouth buffaloes caught in Pasqua and Echo Lakes in 1955 and 1956. Points represent average standard length at half-inch fork length intervals. Curve B — relationship of fork length to weight for 827 bigmouth buffaloes caught in Pasqua and Echo Lakes in 1955. Points represent average weight at half-inch length intervals.

Relation of Growth in Fork Length to Growth in Weight

Measurements of fork length and weight were determined for 827 buffaloes collected in Pasqua and Echo Lakes in 1955. The curve of length–weight relationship (Fig. 3) has been calculated (following Ricker, 1958) as having the formula:

$$w = 0.00097\ l^{2.91}$$

The largest buffalo recorded during the study was a female 31.1 inches (790 mm) long, weighing 25.5 lb (11.6 kg). The longest male measured was 26.1 inches (663 mm), whereas several females of greater length were noted, indicating

that females reach a larger size than do males. Eddy and Surber (1947) report a bigmouth buffalo over 4 ft (122 cm) long, weighing 63 lb (29.5 kg) from the Mississippi drainage, and Harlan and Speaker (1956) report one over 80 lb (36 kg) from Spirit Lake, Iowa.

Growth of Young-of-the-Year

Young buffaloes were caught in substantial numbers in Pasqua Lake during July and August 1956. Length measurements of 241 are shown in Fig. 4. The curve of average growth through the summer, when extended to the early part of the season, suggests that hatching occurred about June 6. Figure 5 shows the appearance of a buffalo 0.7 inch (18 mm) long.

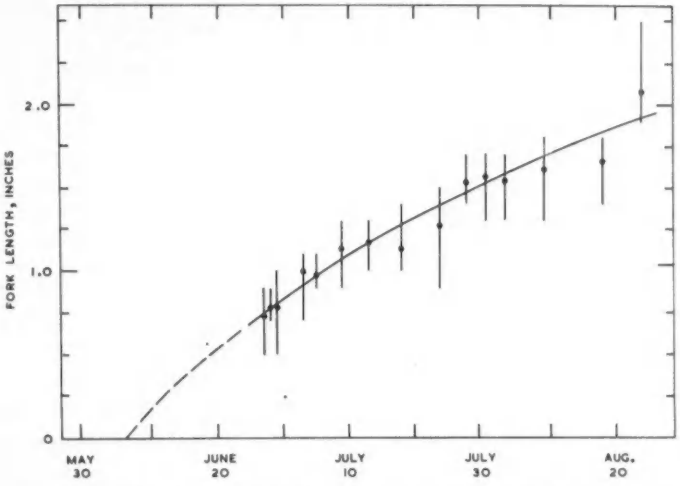

Fig. 4. Growth of 241 bigmouth buffalo young-of-the-year captured in Pasqua Lake in 1956. Points are averages and vertical lines ranges.

The scales of the largest fish from each source used in the preparation of Fig. 4 showed no evidence of an annual ring. Figure 8a shows a scale from a fish 2.5 inches (63 mm) long, the largest young-of-the-year captured in Pasqua Lake in 1956.

Thirteen young buffaloes captured in the Qu'Appelle River on August 28, 1958, had an average length of 2.8 inches (71 mm). This is rapid growth compared to that of young buffaloes in Pasqua Lake in 1956.

Length–Frequency Distribution

Buffaloes (other than young-of-the-year) measured during the study in sufficient numbers to show definite length groupings, were captured only in the 5-inch mesh nets in Pasqua and Echo Lakes in 1955 and 1956, and in the commercial fishery trap in Pasqua Lake in 1956. The numbers of fish measured from each of these 5 sources are as follows: 1955, Echo Lake 5-inch mesh nets

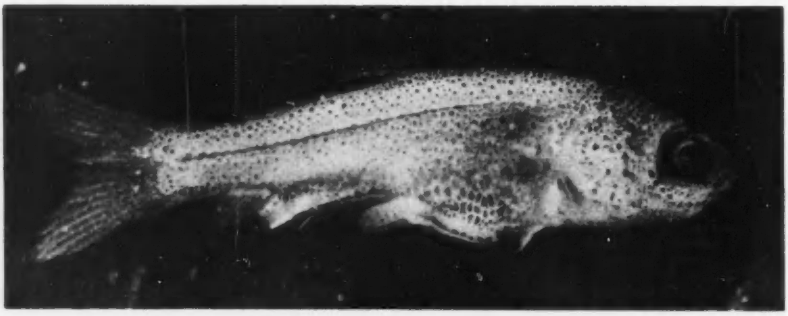

FIG. 5. Bigmouth buffalo 0.7 inch (18 mm) in fork length, captured in Pasqua Lake June 27, 1956.

453 fish; Pasqua Lake 5-inch mesh nets 315 fish; 1956, Echo Lake 5-inch mesh nets 443 fish; Pasqua Lake 5-inch mesh nets 334 fish; Pasqua Lake commercial trap 735 fish. The length–frequency distribution of these fish is seen in Fig. 6 and 7, grouped into length intervals of 0.3 inch (7.6 mm). Figures 6 and 7 include fish from the smallest measured up to 18.0 inches (457 mm). Of the above total of 2280 fish measured, only 29 were in the length range of 18.1–27.6 inches (460–700 mm) and have been omitted from the figures as unimportant in the length–frequency distribution.

Gill nets are usually quite selective of the size of fish captured by a particular mesh size. The size of buffaloes captured in 1956 by 5-inch mesh nets, however, increased noticeably over the size caught by the same gear in 1955 (Fig. 6). This suggests the presence of a distinct and identifiable group of fish, which was sampled in both years. Three considerations indicate that the fish caught by 5-inch mesh nets were representative of the greater part of the population present in each year.

1. The smallest buffalo caught in 5-inch mesh nets in 1955 was 11.6 inches (295 mm) long. Several nets of 3- and 4-inch mesh were set, and numerous seine hauls (not greatly selective as to size of fish caught) were made, capturing only 7 fish ranging from 10.5 to 11.5 inches (267–292 mm). In 1956 the smallest buffalo caught in 5-inch mesh nets was 12.9 inches (328 mm), while 11 fish were captured between 12.0 and 12.8 inches (305–325 mm) by means of small-mesh nets and seines. No buffaloes between age-group 0 and the minimum sizes outlined were captured in 1955 and 1956. Presumably the 5-inch nets in these two years effectively sampled the smaller sizes of buffaloes in the lake.

2. In 1956 the length distribution of fish caught by 5-inch mesh nets in Pasqua and Echo Lakes is similar to that of the less selective commercial trap in Pasqua Lake (Fig. 7). The mode of all 3 distributions is at 14.9 inches (379 mm).

3. In 1956 the mode of the length distribution of fish caught in 5-inch mesh nets in both lakes is higher than in 1955 (Fig. 6). This is evidence of a real increase in the size of the fish present in the lake. If a new year-class had entered the fishery in 1956, the length distribution curves would have been similar in both years.

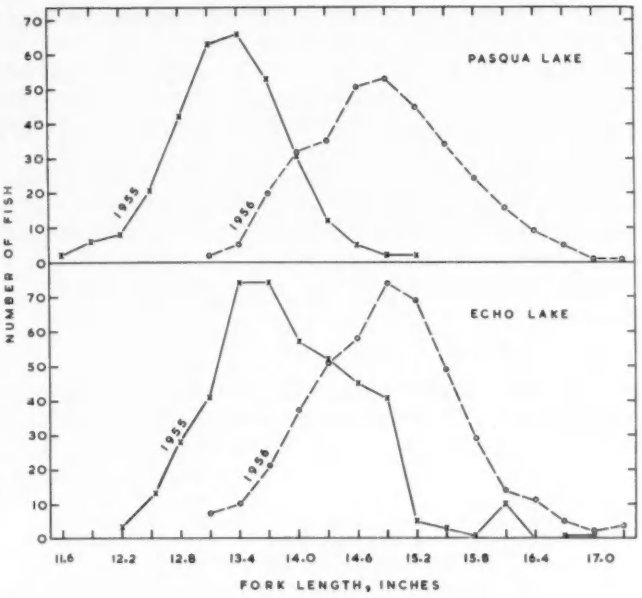

FIG. 6. Length–frequency distribution of bigmouth buffaloes caught in 5-inch mesh nets in Pasqua and Echo Lakes, 1955 and 1956.

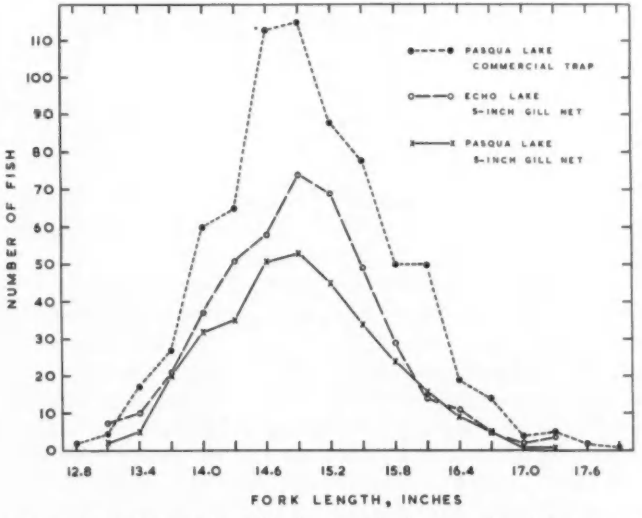

FIG. 7. Length–frequency distribution of bigmouth buffaloes caught in 1956 by 5-inch mesh gill nets in Pasqua and Echo Lakes, and by commercial trap in Pasqua Lake.

The failure of recruitment in 1956 to fill in the size groups vacated by growth of fish since 1955 indicates that one or more dominant age-groups were passing through the fishery. Since the mode of the length distribution in both lakes increased from 13.4 inches (340 mm) in 1955 to 14.9 inches (379 mm) in 1956, the group grew about 1.5 inches (38 mm) in this period.

Age-group Designation

Age determinations were made by interpreting the number of annular marks on the scales. The age-group into which a fish is placed indicates the number of winters through which that fish has passed. For example, a fish in age-group 3 has lived through 3 complete winters, and is in the 4th summer of life (no samples were obtained during the winter).

Validity of the Annulus

Length–frequency distribution of buffaloes caught in 5-inch mesh nets in 1955 and 1956 showed that 98% of the fish ranged in length from about 10.5 to 19.0 inches (267–482 mm). The ages of 275 fish of this group from Pasqua Lake were determined (Table IV). In 1955, 7-year-old fish formed 88% of this group,

Table IV. Age composition of 275 bigmouth buffaloes in the length range of 10.5–19.0 inches (267–482 mm), captured in Pasqua Lake in 1955 and 1956.

Age	1955	1956	1955	1956
	no.	*no.*	%	%
6	4	...	2.5	...
7	139	6	88.0	5.1
8	12	96	7.6	82.1
9	2	15	1.3	12.8
10	...	...	...	...
11	1	...	0.6	...
Total:	158	117	100.0	100.0

while in 1956, 8-year-olds formed about 82% of the sample. The addition of 1 annulus from 1955 to 1956 in the majority of these fish is evidence that the mark assumed to be the annulus is a true year mark.

The fish 7 years old in 1955 and 8 years old in 1956 were hatched in 1948. If the 1948 year-class was as abundant as it appeared in 1955 and 1956, it would dominate the buffalofish populations in past and future years. To test this proposition, scale samples from Pasqua Lake in years other than 1955 and 1956, and from other lakes, were collected. These samples were obtained by lake survey crews and miscellaneous investigations from 1951 to 1958. All scales available were used and were not selected in any way except from the Echo Lake sample of 28 fish. These were selected as representative of the smallest sampled to the 20.0-inch (508-mm) size collected in 1955. Readings of these scale samples appear in Table V, where the year-class to which an age-group belongs is indicated in the last column. It is obvious that in recent years the 1948 year-class far

outnumbered all other year-classes in the samples not only in Pasqua Lake, but in Last Mountain, Buffalo Pound, Echo and Crooked Lakes as well. The persistency of this year-class, as determined from scales, is further evidence that the annulus is a true year mark. Photographs of scale impressions from fish of the 1948 year-class are shown in Fig. 8b and c.

TABLE V. Age composition of bigmouth buffalo samples other than from Pasqua Lake in 1955 and 1956. The 1948 year-class is predominant.

Year	Age	No. of fish	Length range		Year-class
	Last Mountain Lake		*inches*	*mm*	
1951	3	**7**	5.6–8.3	142–211	1948
	12	1	21.8	554	1939
	14	1	22.0	559	1937
	15	1	21.7	551	1936
1952	4	**4**	10.1–13.2	257–335	1948
	12	4	20.5–24.6	521–625	1940
	13	2	22.0–22.5	559–572	1939
	15	1	24.0	610	1937
	18	2	24.5–25.5	622–648	1934
	19	1	26.3	668	1933
	Pasqua Lake				
1952	4	**9**	10.3–14.0	262–356	1948
	5	2	10.8–13.3	274–338	1947
	14	1	26.0	660	1938
1953	5	**14**	11.0–15.7	279–399	1948
	6	1	11.4	290	1947
	7	1	13.6	345	1946
	17	1	26.7	678	1936
	20	1	27.4	696	1933
1957	9	7	14.8–18.7	376–475	1948
1958	9	1	17.5	445	1949
	10	**12**	15.5–18.2	394–462	1948
	11	1	16.9	429	1947
	17	1	25.7	653	1941
	19	1	26.8	681	1939
	Buffalo Pound Lake				
1953	5	**13**	9.4–11.5	239–292	1948
	Echo Lake (see text)				
1955	7	**25**	11.8–16.9	300–429	1948
	8	3	13.0–15.1	330–384	1947
	Crooked Lake				
1956	8	**12**	14.7–19.0	373–483	1948
	9	2	17.3–18.7	439–475	1947

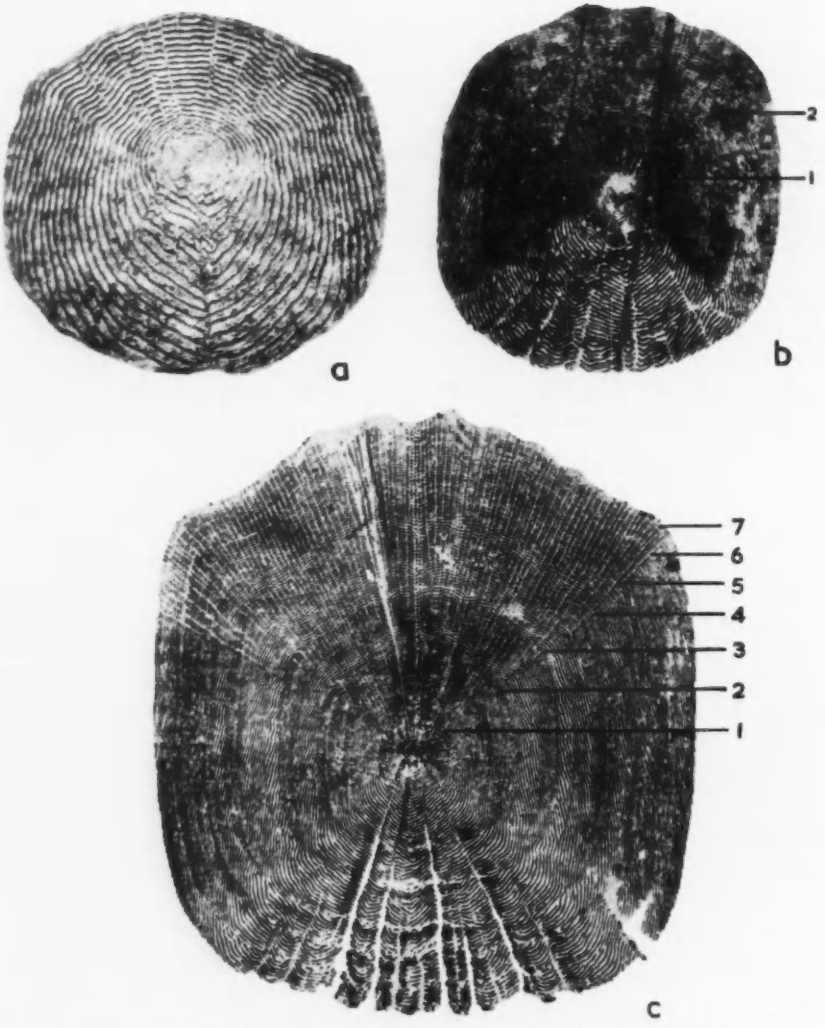

FIG. 8. Photographs of bigmouth buffalo scale impressions. a, from fish 2.5 inches (63 mm) long, no annulus formed. Captured August 24, 1956, the largest fry taken in Pasqua Lake in that year. × 21. b, from fish 8.0 inches (203 mm) long taken May 22, 1951, in Last Mountain Lake. Age 3, the 1951 annulus not yet formed. × 7. c, from fish 14.0 inches (356 mm) long taken June 28, 1955, in Pasqua Lake. Age 7, the 1955 annulus just formed on the scale margin × 6.

Characteristics of the Annulus

The annulus appears as a result of resumption of growth of the scale in summer after cessation of growth during the winter and spring months. In the anterior field it appears as a disorganization in the arrangement of circuli, often accompanied by a noticeably wide space, bordered on the inside with closely spaced circuli and on the outside with widely spaced circuli. Along the antero-lateral ridge, the newly formed circuli 'cut over' those laid down during the previous season. In the lateral fields the circuli are inflected (i.e. they change direction and spacing) as they pass across the annulus, although anastomosis (cutting over) may be pronounced here also. Since buffaloes have a cycloid scale, the annulus is sometimes discernible in the posterior field.

Annuli representing later years are more closely spaced and less distinct than those formed in early years when the scale grows more rapidly. Confidence in assigning ages is claimed for fish 10 years old or younger, while age determinations over 10 years are progressively less reliable as the fish become older.

Time of Annulus Formation

The time of annulus formation was determined from fish collected in Last Mountain Lake in 1951, Pasqua Lake in 1955 and 1956, and Crooked Lake in

Table VI. Time of annulus formation on scales of the bigmouth buffalo in Saskatchewan.

			Dates when scales had *not* formed a marginal annulus		Dates when scales *had* formed a marginal annulus	
Lake	Year	Age of fish	Date	No. of specimens	Date	No. of specimens
Last Mountain	1951	3	May 22	1	...	
			June 14	3	June 14	3
Pasqua	1955	6–9	May 1–25	79	...	
			June 2–14	27	...	
			June 16	16	June 16	5
			June 17	1	...	
			...		June 22, 28	12
			...		July 5–23	12
			...		Aug. 13, 26	5
	1956	7–9	May 26, 29	8	...	
			June 1, 4	21	...	
			...		June 12, 18	3
			June 19	3	...	
			...		July 1–27	41
			...		Aug. 7–31	41
Crooked	1956	8, 9	June 13	5	...	
			...		June 26	1
			...		July 10–20	7
			...		Aug. 22	1

1956. Fish older than 9 years were unsuitable for this purpose, the last annulus being too close to the edge of the scale to tell with certainty whether it was formed in the current or preceding year. Information on the period in which annuli were formed is summarized in Table VI.

Generally, the annulus forms during the second or third week in June in buffaloes from these lakes. The earliest date of annulus formation was June 12, and the latest date on which no formation had occurred was June 19, both pertaining to fish from Pasqua Lake in 1956. Figure 8c shows a scale from a fish captured June 28, 1955, in which the newly formed annulus is visible near the margin.

Beckman (1943) found that the annulus on the scales of Michigan game fish formed between the fourth week in April and the third or fourth week in May. He demonstrated that annulus formation is correlated with temperature and occurs distinctly earlier in the southern than in the northern part of the state. Kennedy (1953) found that annulus formation in Great Slake Lake whitefish occurred shortly after June 20. Time of annulus formation in Saskatchewan buffaloes is intermediate between Great Slave Lake whitefish and Michigan game fish, as might be expected from the intermediate latitude occupied by the Qu'Appelle Lakes.

Growth of the 1948 Year-class

Growth of the 1948 year-class (Fig. 9) has been followed in Pasqua Lake from samples obtained from 1952 to 1958 (no samples were taken in 1954). The

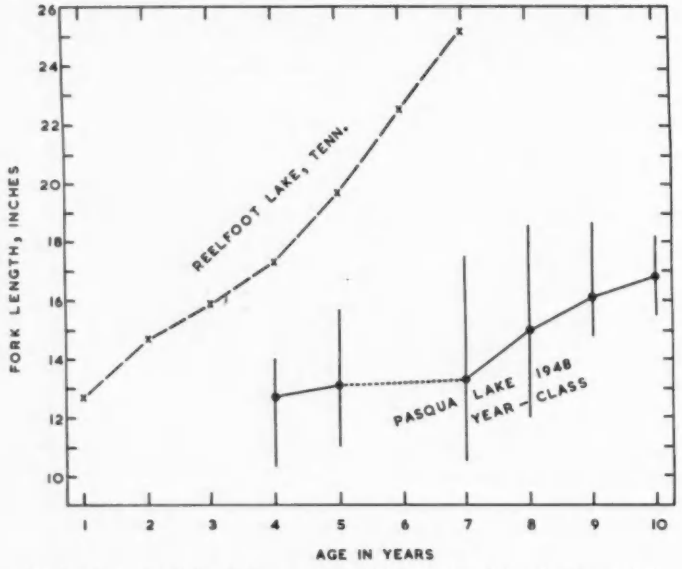

FIG. 9. Growth of the 1948 year-class of bigmouth buffaloes in Pasqua Lake, with data from Reelfoot Lake for comparison. Points are averages and vertical bars are ranges.

number of samples available in each year may be seen in Tables IV and V. For comparative purposes, the growth of bigmouth buffaloes in Reelfoot Lake, Tennessee (Schoffman, 1943) is included in Fig. 9. Growth in Pasqua Lake is exceedingly slow as compared with that in Reelfoot Lake; fish 3 years of age in the latter lake are nearly as long as fish 9 years old in Pasqua Lake.

The slow growth in Pasqua Lake is probably influenced by two main factors, climate and population density. In the Qu'Appelle Lakes this species may be near the northern limit of suitable temperature conditions, and slower growth would be expected. Very slow growth was exhibited in Pasqua Lake from 1952 to 1955, after which an increase in growth rate occurred. It is probable that overcrowding of the abundant 1948 year-class was a factor contributing to slow growth in the first period, with the increase from 1956 to 1958 partially brought about by thinning of the population through fishing and natural mortality.

FOOD STUDIES

The limited attention in the literature to food habits of the bigmouth buffalo has been summarized by Moen (1954). He concluded from analysis of 184 specimens from several Iowa lakes that it is predominantly a plankton feeder rather than a bottom feeder. The principal food was small crustaceans (Entomostraca): in stomachs of 4 fish, entomostracans were numerous while algae were absent, although algae were abundant in plankton hauls on the same day. He suggests that buffaloes either select Entomostraca from plankton or seek out swarms of Entomostraca free of algae. Scidmore and Woods (1960) found that the diet of bigmouth buffaloes in Clear Lake, Minnesota, was principally cladocerans and copepods. Sand formed 40% by volume of the intestinal content of 75 buffaloes less than 10 inches (25 cm) in length.

Food of Young-of-the-year

Analysis of intestinal contents of 114 buffalo young from Pasqua Lake was carried out (Table VII). Fork length of these fish ranged from 0.5 to 1.8 inches 13–46 mm). Only 3 of the fish examined had no food in the digestive tract.

Cladocera and copepods were the most important foods, contributing 71% of the food volume in 1955, and 88% in 1956. Chironomid larvae were next in importance, forming 17 and 7% in 1955 and 1956, respectively. Minor quantities of aquatic beetles, amphipods, nauplii, and ostracods were eaten, along with traces of other animals. Phytoplankton, mainly diatoms, formed 4.4% of the food volume in 1955, but was negligible in 1956.

In the 1956 analysis, *Leptodora* was recorded separately from the other Cladocera, and harpacticoid copepods from the other Copepoda. Little or no *Leptodora* was eaten by most groups, although on June 20 they formed 13.4% of the food of 5 fish, indicating some feeding on active limnetic plankton. Minor amounts of creeping harpacticoid copepods were eaten, demonstrating some feeding on bottom-dwelling plankters.

TABLE VII. Percentage volume of food items eaten by 114 young-of-the-year bigmouth buffaloes from Pasqua Lake, 1955 and 1956.

	1955	1956
No. of stomachs empty	1	2
No. of stomachs with food	41	70
Insects:		
Chironomid larvae	16.7	7.1
Chironomid adults	–	1.3
Coleoptera larvae	0.1	trace
Coleoptera adults	3.6	–
Hemiptera	0.5	trace
Miscellaneous[a]	–	0.3
Hydrachnids	–	trace
Rotifers	–	trace
Crustacea:		
Amphipods	0.4	3.2
Ostracods	–	0.2
Cladocera	30.8	
Leptodora		1.1
Other		28.7
Copepods	40.4	
Harpacticoid		0.2
Other		57.9
Nauplii	3.1	–
Phytoplankton	4.4	–

[a]Includes terrestrial beetle larvae, mosquito larvae, and unidentified insect remains.

FOOD OF JUVENILES AND ADULTS

Food items eaten by buffaloes larger than young-of-the-year were determined for 201 fish captured in Pasqua and Echo Lakes during 1955 and 1956 (Table VIII). The fish ranged in fork length from 10.5 to 28.6 inches (267–727 mm). In 1955 the samples were taken from June to August, and in 1956 during May and June.

The first two columns of Table VIII itemize the foods eaten by all sizes of buffaloes in Pasqua and in Echo Lakes. Entomostraca were the most important items, providing about 75% of the food in both lakes. Chironomids formed 12 and 15% of the food in Pasqua and Echo Lakes, respectively. Other animals, eaten in small quantities, included aquatic beetles, aquatic bugs, molluscs, and amphipods. Plant material, mainly diatoms, was negligible in intestines of fish from both lakes. The only noticeable difference between the lakes was that ostracods were well represented (12.9%) in food of Pasqua Lake fish, but were

unimportant (2.4%) to Echo Lake fish. This may be related to the large area of marsh at the west end of Pasqua Lake associated with the river, where ostracods are abundant.

The next 4 columns of Table VIII show monthly variations in food consumption, information from both lakes being combined. There is an increasing dependence on cladocerans and copepods as the summer progresses. The most striking feature is the paucity of chironomids eaten in June, and the absence of these from the diet of fish captured in August. The unimportance of chironomids in these two periods may be due to emergence of shallow-water species at these times, but may be a change in feeding habits.

The food preference of fish in different size groups is seen in the last 3 columns of Table VIII. There is a distinct trend towards greater dependence on chironomids and less on Entomostraca with increasing size of fish, although in all size ranges Entomostraca make the greatest contribution.

TABLE VIII. Percentage volume of food items eaten by juvenile and adult bigmouth buffaloes captured in Pasqua and Echo Lakes, 1955 and 1956.

Lake:	Pasqua	Echo	Pasqua and Echo				Pasqua and Echo		
Period:	Both Years		May	June	July	August	Both years		
Length: *inches*							10.5–15.0	15.1–20.0	20.1+
mm							267–381	383–508	510+
No. of samples	97	104	27	95	51	28	128	31	42
Insects:									
Chironomids[a]	11.9	15.2	20.0	8.8	28.0	...	8.9	12.5	26.1
Coleoptera[a]	2.3	1.5	4.2	1.5	1.5	...	2.0	3.8	0.4
Hemiptera[a]	0.5	0.1	...	0.5	0.3	0.1	0.6	0.1	...
Molluscs:									
Sphaeriids	3.2	2.7	3.6	3.4	3.0	...	3.4	3.1	1.7
Gastropods	1.9	2.8	6.5	1.9	1.7	...	2.2	3.4	2.1
Miscellaneous[b] and unidentified	1.7	0.1	0.4	1.6	...	...	0.5	2.3	0.8
Crustacea:									
Amphipods	0.9	1.5	4.1	0.7	0.3	0.5	1.0	0.5	2.1
Ostracods	12.9	2.4	12.0	11.0	0.3	...	8.1	6.8	7.9
Cladocera	47.9	55.3	33.3	51.3	52.8	78.1	55.9	55.0	37.4
Copepoda	15.7	17.5	15.5	17.8	11.5	21.1	16.5	11.5	20.3
Phytoplankton:	1.1	0.9	0.4	1.5	0.6	0.2	0.9	1.0	1.2

[a]Mostly immature stages.
[b]Includes Odonata, biting midge larvae, nematode worms, conchostracans, and leeches.

Method of Feeding

Analysis of the diet of young, juvenile, and adult buffaloes in Pasqua and Echo Lakes has revealed that many animals classed as bottom fauna are often taken as food. These bottom organisms include chironomid larvae, miscellaneous insects, molluscs, amphipods, and ostracods. The largest volume of food, however, was composed of Cladocera and copepods. While these are normally thought of as planktonic, there are members of both groups which are classed as "creepers", and which spend a great deal or all of their life on a substrate. To clarify knowledge of the feeding method of buffaloes, it is desirable to know the habits of the entomostracans eaten. Identifications of these animals were made from stomachs of 2 of age-group 0, and 8 older buffaloes captured in 1956 (Table IX).

The animals are classed in one of three categories according to habits and habitat. The first category is of animals which are benthic and littoral, including those associated with weeds or a substrate such as bottom mud. The second category includes animals which are found both as benthos and plankton. The third group is of animals truly planktonic, floating freely most or all of their life. The assignment of animals to each classification is based upon information from Pennak (1953), Smyly (1958), and from observations by Dr E. B. Reed (personal communication).

Of the 20 groups of Entomostraca recognized, the largest number (11) was in the first (benthic and littoral) category, 5 were in the second or "mixed" group, and 4 were "planktonic only". In only one fish, captured June 10, does the largest number of organisms eaten belong to the "planktonic only" group, while in 5 fish benthic organisms predominate. The capture of Entomostraca by buffaloes is therefore by both bottom and limnetic feeding.

Reports of the actual mechanisms of feeding are rare. Forbes and Richardson (1920) from reports by fishermen, suggest that buffaloes search for small molluscs and insect larvae living in the mud. Canfield (1922) writes that buffaloes (species unidentified) feed by working over bottom soil and ooze to obtain small aquatic animals; they also rise to the surface to feed amid floating vegetation.

Feeding of non-captive buffaloes was observed only once during this study. In June of 1956 several fish were observed swimming at an angle of about 55° to the bottom, bouncing with short up-and-down movements as they proceeded along the bottom, both forward and backwards, in a manner best described as "skipping". As the fish contacted the bottom, swirls of muddy water were raised in a search for food through the mud and debris. In the hatchery, captive buffaloes have often been observed feeding on fish-food pellets. They swim forward, at an angle of about 55°, along the bottom of the holding tank littered with food particles. A clear pathway appears behind the fish, as the food is sucked up with much the same effect as a vacuum cleaner.

The gill rakers of buffaloes are well adapted to retain small food particles such as entomostracans as water passes through the gill clefts. Gill rakers of this species are long and closely spaced (Fig. 10a), each gill arch having well-developed rakers extending in opposite directions. Each gill raker has numerous

TABLE IX. Occurrence of different groups of Entomostraca in stomachs of 2 young and 8 older bigmouth buffaloes in Pasqua and Echo Lakes, 1956 (A — abundant; C — common; O — occasional; R — rare; P — present).

	Juveniles and adults								Young	
	Echo May 24	Pasqua May 26	Pasqua May 26	Pasqua June 4	Pasqua June 4	Pasqua June 10	Echo June 26	Echo June 29	Pasqua June 27	Pasqua June 27
(1) *Benthic animals* (in mud and weeds)										
Macrocyclops albidus	C	...	...	...	...	...	...	...	...	...
Eucyclops agilis	C	R	...	...	...	...	...	...	...	P
Eucyclops speratus	...	...	...	...	R	...	...	...	...	...
Simocephalus vetulus	...	...	...	O	...	...	...	...	...	...
Harpacticoida	R	...	R	A	O	P	...	...	...	P
Pleuroxus procurvatus	...	...	C	...	...	...	...	...	P	...
Pleuroxus aduncus or *trigonellus*	...	...	...	...	...	...	...	...	P	P
Leydigia (quadrangularis?)	...	...	...	...	...	...	...	...	P	...
Scapholeberis (mucronata?)	...	...	...	...	...	...	...	...	P	...
Alona sp.	...	...	...	R	...	...	...	...	...	...
Ostracoda	...	...	...	O	A	...	...	...	...	...
(2) *Both benthic and planktonic*										
Acanthocyclops vernalis	...	P	...	O	...	...	A	...	P	...
Daphnia schodleri	...	C	C	O	...	...	O	...	...	...
Chydorus sphaericus	...	...	C	A	C	...	...	...	P	...
Daphnia galeata mendotae	...	...	...	...	...	...	A	P	...	...
Diaphanosoma brachyurum	...	...	...	...	...	...	...	...	P	...
(3) *Planktonic animals*										
Acanthocyclops thomasi	...	R	...	...	...	P	...	...	...	...
Mesocyclops edax	...	...	...	...	...	P	...	P	...	...
Diaptomus sp.	...	...	...	...	...	P	...	...	...	...
Ceriodaphnia sp.	...	...	...	R	...	...	O	...	...	P

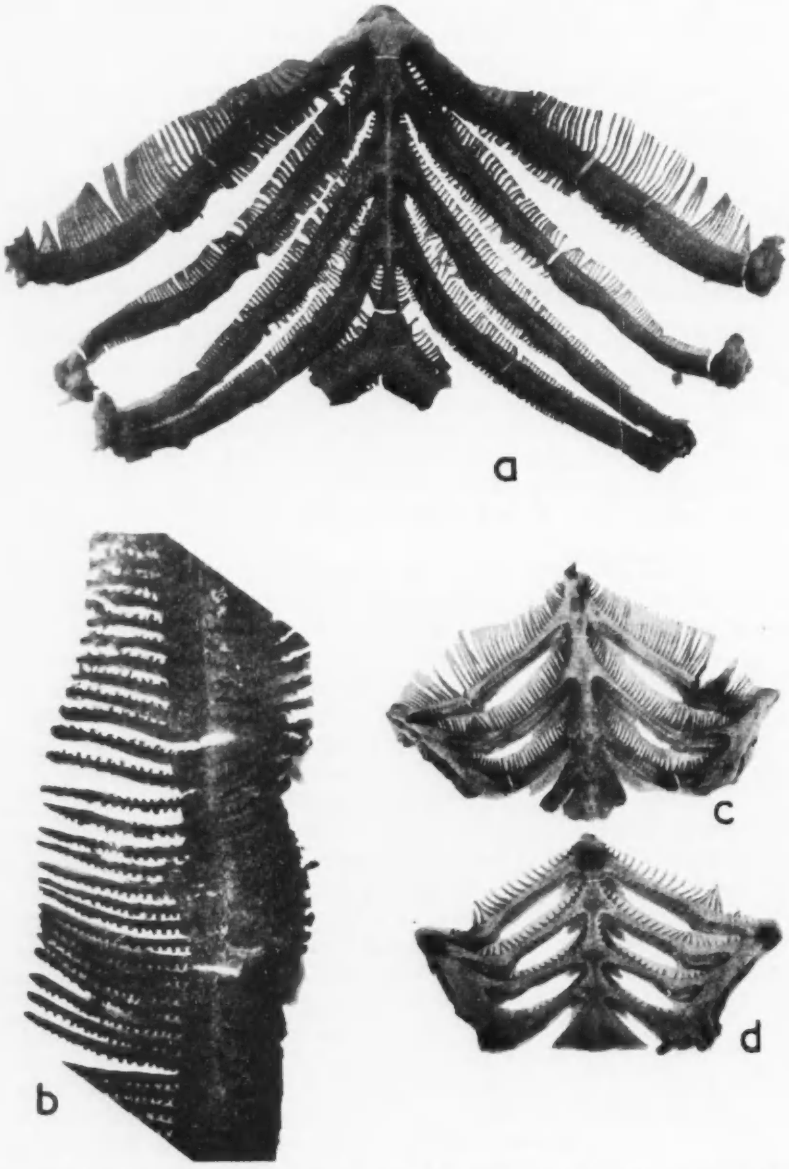

FIG. 10. Gill raker systems of three species of fish. a. Bigmouth buffalo, a bottom and plankton feeder. b. Enlargement of section of a, showing accessory teeth on gill rakers. c. Cisco, a plankton feeder. d. Whitefish, a bottom feeder.

lateral and often bifurcate projections on the edge next the buccal cavity, shown in greater detail in Fig. 10b. Measurement of these projections were made on a gill raker from the centre of the first gill arch of a buffalo 12.7 inches (323 mm) long, using an ocular and stage micrometer. The projections were from 0.20 to 0.25 mm long, the spaces between being about 0.30 mm wide.

The gill raker system of the bigmouth buffalo has the appearance of being a more efficient plankton strainer than that of the cisco (Fig. 10c) which is usually a plankton feeder. Gill rakers of a lake whitefish, a species which usually feeds on macroscopic bottom animals, are shown in Fig. 10d. Both coregonines have minute projections on the gill rakers which, unlike those of buffaloes, terminate as discrete spines. The spines from a gill raker taken from the centre of the first gill arch of a 16.1-inch (409-mm) cisco were about the same length and distance apart as the projections on the buffalo gill raker. However, the spines of the cisco and whitefish project parallel rather than perpendicular to the gill raker, and are possibly less useful in food collecting than those of the buffalo.

Although the percentage of food items in daily samples was not calculated in samples of fish caught on one particular day and location, the food eaten tended to be similar in all stomachs. This was true of both young and older buffaloes, and suggests that the diet is influenced by what foods are available, rather than a search for particular foods.

It is concluded that the bigmouth buffalo occupies a food niche overlapping both bottom feeders and limnetic plankton feeders.

SPAWNING AND REPRODUCTION

Size at Sexual Maturity

Size at sexual maturity for buffaloes in Pasqua and Echo Lakes is seen in Table X, which includes fish up to 18.9 inches (480 mm). The upper limit was chosen because all larger fish examined were mature; the largest immature fish seen was a female of 18.7 inches (475 mm), captured May 31, 1957, in Pasqua Lake. Two females, 15.4 and 16.7 inches long (391 and 424 mm), both of the 1948 year-class, were still immature when examined May 29, 1959.

Males reach sexual maturity at a considerably smaller size than do the females. From 1955 to 1957, the condition of the gonads of 360 females less than 19 inches (482 mm) long (probably from 7 to 9 years old) was determined, and of these only 19 were mature. Males began to mature in the range 12.0–12.9 inches (305–328 mm); in the range 14.0–14.9 inches (356–379 mm) the majority were mature.

Canfield (1922) found that buffaloes reared in ponds spawned when 4 years old. Swingle (1957) found that ". . . bigmouth buffalo one or more years old and weighing 1 pound or more were found to be satisfactory for brood fish". Compared with buffaloes from other areas, the maturation of females in Pasqua and Echo Lakes is extremely slow, both in age and size at maturity. This unusual situation may be the corollary of the slow growth, due both to the density of the 1948 year-class, and the cooler temperatures at this latitude.

TABLE X. Size at sexual maturation of bigmouth buffaloes captured in Pasqua and Echo Lakes, 1955 to 1957. All fish examined which were 19.0 inches (483 mm) and larger were mature (I = immature; M = mature).

Length group		Female						Male					
		1955		1956		1957		1955		1956		1957	
		I	M	I	M	I	M	I	M	I	M	I	M
inches	mm												
11.0–11.9	279–303	6	..	..	..	..	..	2	..	..	..	..	..
12.0–12.9	305–328	54	1	9	..	..	..	35	11	3	1	..	..
13.0–13.9	330–353	109	2	40	1	..	..	54	29	23	15	..	..
14.0–14.9	356–379	30	1	34	5	4	..	9	9	49	46	1	4
15.0–15.9	381–404	2	1	36	2	6	..	1	2	24	36	1	8
16.0–16.9	407–429	..	..	8	2	1	..	..	..	1	5	..	3
17.0–17.9	432–455	..	..	1	2	..	..	1	1	..	2	..	..
18.0–18.9	457–480	..	1	..	1	1	..	..	2	..	4	..	..

SPAWNING

Spawning of the bigmouth buffalo has been described by Mosher (1885) and Canfield (1922) as a rather noisy, obvious performance which involves much splashing in water a few feet deep. Canfield reported that spawning starts at 58° F (14.4° C), but is slow until water temperatures reach 60–62° F (15.6–16.7° C). Swingle (1954) found that eggs were laid at 60–80° F (15.6–26.7° C), with heaviest spawning at 60–65° F (15.6–18.3° C). Canfield found that most of the eggs adhered to floating vegetation, while Swingle recommends that ponds have a cover of weeds or grass before being flooded for spawning areas. Both Canfield (1922) and Swingle (1957), in describing pond culture of buffaloes, note that introduction of fresh water, either by flooding the spawning pond or transferring the fish to ponds with fresh water, is necessary to activate spawning. Canfield thought that the flooding of ponds which initiated spawning was analogous to the normal spring floods of the Mississippi drainage. Swingle suggests that the overwintering buffaloes produce sufficient excretions to repress reproduction, and that addition of fresh water dilutes the repression factor.

During 1955 and 1956 spawning activities such as described above were not observed in Pasqua and Echo Lakes. In both years the survey was in progress when the ice disappeared. At this time and for a month or more later, attempts to observe spawning were made in the shallow areas of both lakes, and for some distance on the flooded land upstream from Pasqua Lake. If spawning is as noticeable as the literature suggests, this activity was not common here in these two years.

Indirect evidence of the spawning period was obtained through examination of the gonads of mature fish (over 47 cm long). In 1955, gonads of 41 female and 63 male buffaloes were examined. Green fish of both sexes were captured as

late as May 18. The first spent fish of both sexes were caught on May 25, and were frequent thereafter. A near-ripe female was captured June 6, and ripe and near-ripe males from April 30 to July 7. The sex ratio of these large fish was 2 females to 3 males.

In 1956 the condition of the gonads of 19 female and 96 male buffaloes of large size was recorded. The last unspawned female was caught on May 23, while numerous ripe and near-ripe males were caught from May 18 to June 26. The first spent fish of both sexes were caught on May 18. The sex ratio was 1 female to 5 males, accounting for the presence of ripe males late in the season.

On May 13, 1957, 10 large buffaloes at the Craven dam were examined. Of these, 6 were green females, 1 a green male, and 3 ripe males.

That spawning of buffaloes was limited during the study is supported by the paucity of young-of-the-year captured, especially in 1955. In that year 56 seine hauls were made in Pasqua Lake, of which only 3 caught a few young buffalo, while 28 seine hauls in Echo Lake caught none. During 1956, reproduction as shown by abundance of young was more successful than in 1955. In Pasqua Lake, 48 of a total of 185 seine hauls captured young buffalo in numbers from 1 to over 200. In Echo Lake 75 seine hauls caught no young, but fry were captured on one occasion with a kitchen sieve.

Egg Size and Fecundity

The average and range of size of eggs (preserved in 5% formalin) from 3 buffaloes are shown in Table XI. In the first column the average diameter of 19 residual eggs from a spent female is 1.5 mm, with a range of 1.2–1.8 mm. In comparison, the average diameter of 24 eggs from a green female is 1.3 mm, ranging from 1.1 to 1.5 mm (second column). This green female was captured May 13, 1957, and would have spawned that spring.

Table XI. Average size and range of size of eggs from three mature bigmouth buffaloes captured in the Qu'Appelle drainage.

Length: *inches*	25.0	26.2	28.6
mm	635	665	727
Weight: *lb*	10.7	14.4	15.5
kg	4.85	6.53	7.03
Date of capture:	June 4, 1955	May 13, 1957	May 18, 1955
Place of capture:	Pasqua Lake	Qu'Appelle River at Craven	Pasqua Lake
Condition of ovary:	Spawned out, only a few mature eggs left	Green, would have spawned in 1957	Eggs developing, would not have spawned in 1955
Number of eggs measured:	19	34	21
Average diameter of eggs (*mm*):	1.5	1.3	0.7
Range of diameter of eggs (*mm*):	1.2–1.8	1.1–1.5	0.6–0.7

In the last column the average diameter of 21 eggs from a fish captured May 18, 1955, was 0.7 mm, with a range from 0.6 to 0.7 mm. It is clear that the eggs of this fish would not have developed in time to be spawned in the year of capture, but would probably have matured and been spawned in the spring of 1956. It appears that all mature female buffaloes in the Qu'Appelle system do not spawn every year. The above fish and two others with ovaries in about the same stage of development, were caught in May during the study.

The estimated number of eggs in the ovaries of the green buffalofish captured May 13, 1957 at Craven dam (see Table XI), is about 750,000, as shown in Table XII.

TABLE XII. Estimated number of eggs in ovaries of a bigmouth buffalo 26.2 inches long weighing 14.4 pounds (665 mm, 6.53 kg), captured in the Qu'Appelle River at Craven May 13, 1957.

Ovary	Volume of eggs counted	Count of eggs	Total volume of ovary	Estimated number of eggs
	cc		*cc*	
A	26.2	23,831	382.2	347,641
B	9.5	9,251	427.5	416,295
A + B:				
By addition				763,936
By calculation	35.7	33,082	809.7	750,322

CORRELATION OF SPAWNING WITH WATER FLOW

The contention by Canfield (1922) that the stimulus to spawning is the normal spring flooding of the Mississippi River receives support from the present study. The occurrence of the numerous 1948 year-class in the Qu'Appelle drainage appears to be correlated with flooding. Table XIII shows the total runoff in the Qu'Appelle River at Craven for the month of May (the month of buffalo spawning as inferred from examination of gonads) from 1944 to 1956. In the period 1944 to 1954 the greatest May runoff occurred in 1948. It is not difficult to envisage production of a strong year-class as was produced when the tremendous fecundity of the buffalo is coupled with conditions favourable to spawning.

Size distribution and age determinations of fish caught by netting and seining in 1955 and 1956, indicate that no appreciable spawning or fry survival occurred in the years 1949 to 1954. The small number of young captured in 1955 indicates rather poor reproduction in this year, with slightly better success in 1956. While 1949 to 1954 were years of negligible to moderate runoff, both 1955 and 1956 were years of violent flooding in the Qu'Appelle Valley. Although water conditions favourable to spawning were met in the latter two years, production of young is less than would be expected under favourable conditions because of the deficiency of mature females in the population.

TABLE XIII. Total runoff in acre-feet during May in the Qu'Appelle River at Craven. (Information from Canada Department of Northern Affairs and National Resources, Water Resources Papers, No's. 97, 101, 105, 109, 113, 117, published in years 1949, 1951, 1953, 1954, 1956 and 1958, and from P.F.R.A., personal communication.) (1 acre-foot = 1233 m³.)

Year	Runoff	Year	Runoff
	acre-feet		*acre-feet*
1944	13	1951	17,160
1945	31	1952	236
1946	455	1953	Nil
1947	5,530	1954	834
1948	39,420	1955	90,400
1949	1,140	1956	62,800
1950	890		

PARASITES

Ectoparasitic copepods were found on buffaloes in Pasqua Lake and in the Qu'Appelle River at Craven. Thirteen parasites from fish caught in Pasqua Lake on October 23, 1957, were identified by Dr P. L. Ilg as *Argulus appendiculosus* Wilson.

A sample of young fish from the Qu'Appelle River between Craven and Pasqua Lake was found to be heavily infected with myxosporidian spores. These were enclosed in prominent white cysts on the gills of the fish, which ranged from 1.8 to 3.4 inches in length (46–86 mm). The smaller fish were more heavily infected than the large ones, and the 3 smallest fish were emaciated, with abnormally large heads. Since the gills of the 3 fish were nearly covered with cysts, the emaciated condition was probably caused by interference with the feeding mechanism. Davis (1953) reports myxosporidian cysts on the gills of smallmouth buffaloes.

ASSOCIATES

The species of fish associated with young buffaloes caught in 51 seine hauls in Pasqua Lake in 1955 and 1956, are shown in Table XIV. The species most often found with these young were yellow perch, white suckers, and spottail shiners, all of which are abundant in the lake (Table I). The absence of coregonines in habitats occupied by young buffaloes is due to the preference of the coregonines for deeper and cooler water during the summer, when the seine hauls were made. The ninespine stickleback, one of the most abundant of the small species, was rarely taken in seine hauls with young buffaloes.

TABLE XIV. Percentage occurrence of species present in 51 seine net catches which captured young bigmouth buffalo in Pasqua Lake, 1955 and 1956.

Young and small species	Percentage occurrence	Juveniles and adults	Percentage occurrence
Yellow perch	73	Northern pike	37
White sucker	63	Buffalo	10
Spottail shiner	57	Yellow perch	6
Emerald shiner	41	Walleye	2
Walleye	39		
Trout-perch	31		
Darters	22		
Ninespine stickleback	14		
Fathead minnow	12		

There was little evidence of predation on young buffaloes, although piscivorous fish were often found with them. During 1955 and 1956, stomach contents of several hundred juvenile and adult pike, and adult walleye and yellow perch, were examined. Only two pike, 10.6 and 11.1 inches long (269 and 282 mm), had eaten small buffaloes, and each pike had only one young in the stomach. The robust shape of buffaloes, in which body depth is greater for length than in many other species, possibly makes them difficult for predacious fish to swallow.

The numbers of larger species captured with juvenile and adult buffaloes in Pasqua and Echo Lakes in 1955 and 1956 are shown in Table XV. Since the associations of fish caught by gill net and seine are different, the catches by each method are tabulated separately.

The fish most abundant in gill-net catches, other than the buffalo, is the walleye. In May, and again in August, coregonines were caught in nets with buffaloes. Lesser numbers of coregonines in June, and their absence in July has been explained above. The presence of northern pike in buffalo habitat in May is likely correlated with the shallow-water spawning of this fish.

The few carp and northern redhorse suckers caught with buffaloes are a reflection of low populations of these fish at the time of sampling. If their numbers increase in future years, a relationship with buffaloes may develop.

The numbers of large fish caught in seines with buffaloes indicate a closer relation with white suckers, perch, and pike than with walleyes. The large number of perch caught in August occurred mainly in two seine hauls in Echo Lake in 1956, when 200 of the 243 fish were captured, unduly emphasizing this association.

The fact that walleyes were caught in gill nets, but to no great extent in seine catches, indicates an offshore overlap of this species with buffaloes. The gill nets were set farther from shore than the limited area sampled by the seine net.

TABLE XV. Numbers of each species of adult and juvenile fish captured with bigmouth buffaloes in Pasqua and Echo Lakes in each month from May to August, 1955 and 1956.

Method of capture	Period	Buffalo	Cisco	Lake whitefish	White sucker	Northern redhorse	Burbot	Northern pike	Walleye	Yellow perch	Carp
Gill net	May	253	38	55	32	–	13	51	26	–	1
	June	347	17	6	31	–	2	4	161	2	–
	July	390	–	–	65	1	–	6	255	12	5
	Aug.	847	51	31	33	1	–	1	136	1	12
Total:		1837	96	92	161	2	15	62	578	15	18
Seine net	May	109	–	–	5	–	1	18	22	5	–
	June	518	6	2	9	–	1	22	2	29	–
	July	18	–	–	–	–	–	8	5	5	–
	Aug.	37	–	–	87	1	–	20	4	243	1
Total:		682	6	2	101	1	2	68	33	282	1

BEHAVIOUR

Bigmouth buffalo have a pronounced tendency to school, a behaviour pattern occurring throughout the summer. From the bow of a moving boat, schools of about 25 fish were often seen swimming in parallel paths away from the course of the boat. They were also seen singly and in small numbers.

On warm still days buffaloes spread out over the entire surface of the lakes where they rest quietly, often in the midst of a dense algal bloom. The upper 2 ft of water is preferred for this "loafing". Often the dorsal fin projects above the water. Representative dates and surface water temperatures in Echo Lake in 1955 when this occurred were: July 26, 22.0° C; August 22, 20.4° C; September 2, 20.0° C. This behaviour was never observed on windy days, for when the water was choppy the buffaloes congregated in protected bays in somewhat deeper water.

No recognizable feeding was observed while the fish were floating near the surface, but this cannot be disregarded as a purpose of this behaviour. Respiratory movements in the midst of dense plankton would provide a certain amount of available food. Food studies suggest that algae are of little importance in the diet but perhaps, as Moen (1954) suggests, they can strain Entomostraca from water containing algae. Further study is necessary to understand the reason for this behaviour.

DISCUSSION

The present study of buffaloes has been largely one of the extremely numerous 1948 year-class. In some ways this unique population structure has been advantageous, and in other ways detrimental, to the study. It has been beneficial in providing opportunity to follow development of annual rings on the scales of one year-class through a series of years, and a help in evaluation of scale reading as a method of age determination. On the other hand, it has been partly responsible for a rather distorted growth rate, an unusual picture of reproduction concerning size at sexual maturation, and possibly a misleading impression of predation on fry.

While population density of buffaloes in these lakes may affect growth and sexual maturation, the influence of geographic location may also be great. Cooler temperatures and a shorter growing season here could produce slower growth and slower maturation than in southern waters. Evidence is presented that some mature females do not spawn every year, a phenomenon which could be the effect of northern location. Kennedy (1953) summarizes evidence that many females in nothern freshwater fish populations tend to spawn at intervals of two or more years, and suggests the cause to be the short growing season.

Size and age distributions of the buffalo population in 1955 and 1956 are abnormal in comparison with that found in most studies of fish, but this is quite possibly the usual condition in the Qu'Appelle Lakes. The successful 1948 year-class was produced under favourable runoff conditions; when the females of this year-class mature and if suitable spawning conditions again prevail, another strong year-class is probable. If heavy runoff is the major factor governing reproductive success, population peaks associated with flood years will be the rule. This leads to the interesting speculation that buffaloes are more typically inhabitants of rivers than of lakes, and that while existence in lakes is possible, a flourishing population must be associated with a river or nearby marsh with regular spring floods. In an intermittent river such as the Qu'Appelle, which in some years ceases to flow for several weeks, the presence of lakes is a necessity for existence. The adaptation to a lake habitat however, may be secondary.

In a limited utilization of the buffalo resource, the commercial fishermen take advantage of the peculiar habit of idling near the surface. If 3 or 4 consecutive still, warm days occur, large numbers of buffalo congregate in the marsh west of Pasqua Lake. A coarse barrier net of 2-inch mesh is then stretched across the entrance to this marsh and when the buffaloes attempt to return to the lake, they are herded into pens in shallow water along the shore.

If sporadically successful reproduction is a normal occurrence in the Qu'Appelle drainage, a depressed growth rate as found in the 1948 year-class may be expected. Under such conditions, the commercial fishery would do well to remove the fish at the smallest size acceptable by the market. The efficiency of the harvest would thus be increased, since annual mortality probably outweighs the annual weight increment of such an overcrowded population. Such exploitation would also leave more room and promote faster growth of the remaining fish.

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Use of Coloured Tags in Fish Population Estimates[1]

By G. H. Lawler and G. F. M. Smith

Fisheries Research Board of Canada
Biological Station, London, Ont.

ABSTRACT

Transparent colourless and opaque yellow tags of several types were applied to small perch, less than 15 cm in length, and larger suckers, 17 cm and greater, in Heming Lake, Manitoba, Canada. The return of opaque yellow tags was significantly smaller than that of clear transparent tags (less than one-half) for the small fish only. Tag type was relatively unimportant. This is interpreted as a higher predation rate, by pike, on small fish with opaque yellow tags.

INTRODUCTION

In 1960 a fish tagging and recovery program was begun at Heming Lake (1 square mile, 260 hectares; Lat. 55°N, Long. 101°W), Manitoba, Canada, to study methods that are or can be used to estimate the parameters of population dynamics of natural populations and their limitations. Several types of tags, both transparent colourless and opaque yellow, were used. On examination, several stomachs of pike, *Esox lucius* L., were found to contain yellow tags. The finding of these tags so soon after application caused some concern, as it introduced the possibility of subsequent inaccurate population estimates if these marked animals stood out from, rather than were assimilated with, the unmarked animals and thus were subject to selective predation.

An experiment to compare the return of coloured and transparent colourless tags was started in 1961 with small fish (which could be more easily preyed upon), and continued in 1962 using larger fish of a size that were unlikely to be subject to such predation.

MATERIALS AND METHODS

The small fish used in the 1961 tagging were yellow perch, *Perca flavescens* (Mitchill), of fork length less than 15 cm. These were abundant in the lake and of a size thought to be preyed upon by the small pike.

The larger fish used in 1962 were white suckers, *Catostomus commersoni* (Lacépède), of fork length 17 cm and over. These fish were thought to be of a size less subject to pike predation than the smaller perch.

The tags used on perch in 1961 were of the following types:

(a) Anchor tag (Lawler, 1963) attached by linkage of stainless steel (type 316 and 1.012 inch diameter), tantalum (1.010 inch diameter), and monofilament nylon (8 lb test).

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(b) Carlin tags (Carlin, 1955) with attachment and linkage of both stainless steel and tantalum as in (a) above. Nylon monofilament linkage was not used on the Carlin tags.

The identifying numbered discs (15 × 5 mm), on both Anchor and Carlin tags, were used in approximately equal quantity of transparent colourless and opaque yellow plastic.

The tags used on suckers in 1962 were of the following types:

(a) Carlin with tantalum attachment and linkage and with approximately equal quantity of transparent colourless and opaque yellow discs as above.

(b) Spaghetti darts modified from description of Yamashita and Waldron (1958) and supplied by Floy Tag Company, Molalla, Oregon, as Catalogue No. FT-6. The double barb moulded nylon dart was about 16 mm long, and the trailing vinyl tubing bearing the identification number was coated to withstand abrasion. Approximately equal quantity of the vinyl tubing trailers were transparent colourless and opaque yellow.

All fish tagged were also fin clipped, so that recaptures that had lost tags were recognizable.

The initial capture and recapture of fish was with non-lethal gear (seines, trap nets and trammel nets), with some lethal recaptures in gill nets. These fish were all tagged in about one week during the spring spawning run and were initially captured for tagging in seines. The fish were anaesthetized with M.S. 222 during tagging and were held in pens until post-tagging recovery was complete — up to 24 hr.

The tagging and recapture of small perch during 1961 were carried on simultaneously throughout the summer, but care was taken to alternate clear and coloured tags and also tag types so that at any time there was approximately a balance. The 1962 recaptures of perch reported were all tagged in 1961. Thus, the 1961 perch recaptures reported here cannot be used directly for population estimates without further time of tagging and recapture correction. All tagging of suckers on the spawning run in 1962 was before any of the recaptures here reported and recaptures were made elsewhere in the lake.

RESULTS AND CONCLUSION

The tagging and recovery data for small perch are presented in Table I and for the larger suckers in Table II. Some appropriate tests of significance are shown. The opaque yellow tags were returned at a significantly lower rate than were the clear transparent tags. This lower return is true regardless of tag type. The various tag types were returned at different rates, some of which are statistically significant but not as important as the colour factor.

For larger suckers, in 1962, there was no significant difference for either tag colour or tag type.

TABLE I. Heming Lake yellow perch, less than 15 cm in length, tagged in 1961 and recaptured in 1961 and 1962.

	Opaque yellow tags				Transparent colourless tags				Total tags			
		Recovered				Recovered				Recovered		
		1961	1962			1961	1962			1961	1962	
Tag type	Tagged quantity	Quantity		Percent total	Tagged quantity	Quantity		Percent total	Tagged quantity	Quantity		Percent total
Anchor stainless	75	2	3	6.6	124	28	28	45.2	199	30	31	30.6
Anchor tantalum	77	5	6	14.3	99	17	21	38.4	176	22	27	27.8
Anchor nylon	31	1	2	9.7	44	4	1	11.4	75	5	3	10.6
Anchor total:	183	8	11	10.4	267	49	50	37.1	450	57	61	26.2
Carlin stainless	84	2	4	7.1	81	2	15	21.0	165	4	9	13.9
Carlin tantalum	79	6	15	26.6	56	8	7	27.0	135	14	22	26.6
Carlin total:	163	8	19	16.6	137	10	22	23.3	300	18	41	19.6
Total:	346	16	30	13.3	404	59	72	32.4	750	75	102	23.6

Clear vs Yellow $\chi^2 = 37.8$ P = < .001 (highly significant).
Anchor vs Carlin $\chi^2 = 4.29$ P = .04 (significant).
Tantalum vs Stainless (overall) $\chi^2 = 1.617$ P = .20.
Tantalum vs Stainless (Carlin) $\chi^2 = 7.6127$ P = .006 (significant).
Tantalum vs Stainless (Anchor) $\chi^2 = 0.356$ P = .50.

TABLE II. Heming Lake white sucker, 17 cm in length and over, tagged in the spring and captured during the summer and fall, 1962.

	Yellow tags			Transparent tags		
		Recovered			Recovered	
Tag type	Tagged quantity	Quantity	Percent	Tagged quantity	Quantity	Percent
Carlin tantalum	200	16	8.0	204	20	9.8
Spaghetti dart	229	22	9.6	225	17	7.5
Total:	429	38	8.8	429	37	8.6

Transparent colourless vs Yellow — not significant.
Carlin vs Spaghetti Dart Type — not significant.

It is concluded that the smaller return of opaque yellow tags on small perch was due to the increased predation by pike on the fish so marked. This is not true for larger fish which are assumed to be much less subject to this predation. It is suggested that caution be used in applying coloured tags to fish that are subject to strong predation, if the results of recaptures are intended for use in population estimates.

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2-Phenoxyethanol as a General Anaesthetic for Sockeye Salmon[1]

By H. S. Sehdev, J. R. McBride and U. H. M. Fagerlund

Fisheries Research Board of Canada
Technological Research Laboratory, Vancouver, B.C.

ABSTRACT

The dose–response relationship of 2-phenoxyethanol, as a general anaesthetic, in adult sockeye salmon (*Oncorhynchus nerka*) has been investigated. At 11° C the effective dose (ED_{50}) and lethal dose (LD_{50}) were approximately 43 and 130 ml/100 Imperial gal, respectively. The therapeutic ratio $\left(\frac{LD_{50}}{ED_{50}}\right)$ was more than 3, indicating a good margin of safety. At a lowered aquarium temperature of 4° C the anaesthetic effects of 2-phenoxyethanol were potentiated. ED_{50} and LD_{50} at this temperature were approximately 25 and 130 ml/100 gal of water, respectively. The therapeutic ratio was more than 5, indicating that the margin of safety was increased by the decrease in temperature.

INTRODUCTION

2-PHENOXYETHANOL has been reported to be an effective chemotherapeutic agent in the treatment of certain infections in fish (van Duijn, 1956; Wolf and Dunbar, 1959). Van Duijn reported that for some fish (unspecified) the lethal dose of this drug was 400 ppm. Its use as an anaesthetic for sockeye salmon (*Oncorhynchus nerka*) originated in this laboratory, following an incidental discovery of its anaesthetic effects (Idler *et al.*, 1961). Since then it has been employed here primarily as an anaesthetic in proceedings requiring handling or prophylactic and curative treatment of fish (Idler *et al.*, 1961; McBride *et al.*, 1963). In conjunction with lowered water temperature (4° C) we have also used it as an anaesthetic when transporting adult sockeye salmon (Idler *et al.*, 1961).

The present report describes results of an investigation in which the effective dose–response relationship (Drill, 1954) and the approximate range of lethal dose both at 11–11.5° C (temperature of aquarium water at the time), and at 4° C (the temperature used during transportation of fish) have been studied.

MATERIALS AND METHODS

2-PHENOXYETHANOL

2-phenoxyethanol is a colourless, oily liquid, with a slightly aromatic odour. It has a molecular weight of 138.16, boiling point of 245.2° C and solubility in water of 2.67% at 25° C. It is marketed in the practical grade by Eastman Organic Chemicals, Rochester, New York. For practical convenience, the concentrations of 2-phenoxyethanol used are given in millilitres/Imperial gal of water. One ml/gal at 20° C is equivalent to 293.0 ppm, assuming 100% purity for the product used.

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Fish

The adult sockeye salmon (*O. nerka*) used in this study were obtained from Great Central Lake, Vancouver Island, B.C. The details of transportation, holding facilities and of the prophylactic salt and antibiotic treatments for control of fungus and other infections have been described previously (Idler *et al.*, 1961; McBride *et al.*, 1962). At the time these experiments were carried out the fish had been held in dechlorinated water with a temperature range of 10–12° C for periods of from 6 to 9 weeks.

EXPERIMENTAL PROCEDURES

Dose–Response Relationship at 11° C

Experiments to determine the dose–response relationship at a water temperature of 11° C were carried out in circular (6 ft diameter fiberglass) holding tanks. Four such tanks containing 9, 12, 18 and 22 fish[2], respectively, were used. At the beginning of the experiment the water supply to the tank was cut off and the volume of water in the tank was reduced to 350 gal. The water was aerated (with air or oxygen) and its temperature during the period of experiment was practically constant (11–11.5° C). A calculated quantity of 2-phenoxyethanol was added to the tank and dispersed by stirring the water with a wooden paddle, and by moving the air line about in the tank. The number of fish that became anaesthetized within the first 90 min was counted. The fish were considered to have been anaesthetized when (a) they turned belly up and in this condition either swam or settled down to the bottom of the tank and (b) their responsiveness to light or touch was reduced to the extent that they could be handled easily. The fresh water supply was then turned on again and the fish were allowed to recover for 24–48 hr before another experiment was carried out

Lethal Dose at 11° C

As the fish used in this work were required for other purposes, it was necessary to establish an approximate range of lethal dose without sacrificing large numbers of fish. To achieve this, fish in batches of 4 and occasionally 8, were transferred to a smaller, rectangular aluminum tank containing 60 gal of aerated water. The first batch of fish was exposed to a relatively low concentration (85 ml/100 gal of water) of 2-phenoxyethanol. In the subsequent batches the concentration was increased in steps of 15 ml/100 gal of water. The duration of exposure in each experiment was 8 hr. The fish were then returned to fresh water. The number of deaths occurring both during the period of exposure to 2-phenoxyethanol and during the following 12 hr in fresh water were noted.

Dose–Response Relationship and the Range of Lethal Dose at 4° C

This series of experiments was carried out in the aluminum tanks described above. The water was chilled to 4° C by leaving it overnight in a cold room and was maintained at this temperature during the experiment by addition of small

[2]There was no particular reason for such a distribution. The fish were obtained from the field in several batches and each batch contained a different number of fish and was held in a separate tank.

amounts of ice prepared from dechlorinated water. The other experimental details were the same as outlined in the foregoing section.

RESULTS

Dose–Response Relationship at 11–11.5° C

Sixty-one fish were used to determine the dose-response relationship. The percentage of fish responding to a given dose of 2-phenoxyethanol is plotted in Fig. 1. The time of onset of anaesthesia varied with the concentration of the anaesthetic used but no attempt was made to study this relationship closely. However, the fish that responded usually did so within 10–30 min, at all concentrations employed. Longer exposure (up to 2 hr) did not increase the number of fish responding. On transferring these fish back to fresh water the apparent recovery occurred within 5–15 min.

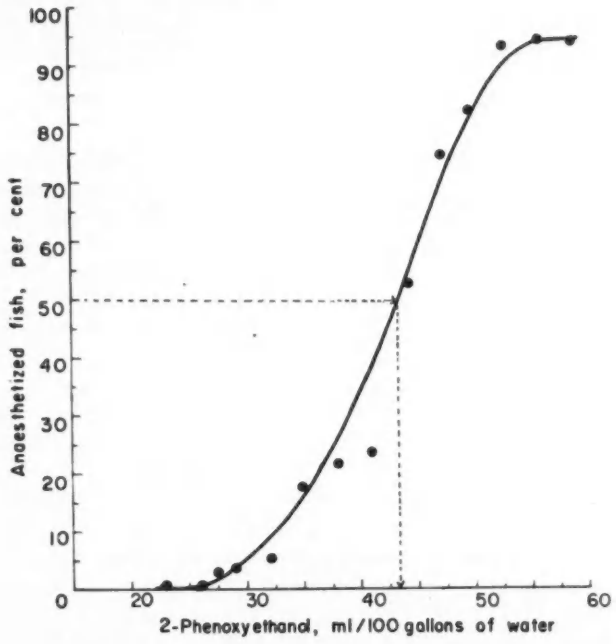

FIG. 1. The dose–response relationship at 11–11.5° C. The broken lines indicate the ED_{50}.

Dose–Response Relationship at 4° C

The fish when transferred from fresh water at 11° C to aerated cold water at 4° C showed a decrease in their spontaneous swimming; however they did not show any signs of anaesthesia (*vide supra*) even after exposures to this temperature for as long as 1½ hr. Addition of 2-phenoxyethanol in much smaller amounts than those used at 11° C at this point produced anaesthesia. Upon return to

fresh water these fish showed apparent recovery from the anaesthesia in approximately the same period of time as did fish that had been anaesthetized at 11° C. The results are summarized in Table I.

Range of Lethal Dose at 11–11.5° C

Thirty-two fish in batches of 4 each, were exposed to a given concentration of 2-phenoxyethanol at a time. The results are presented in Table II. The approximate range of concentration in which mortalities began to occur was between 130 and 145 ml/100 gal of water. In the fish at the latter concentration gill movements stopped after 1½ hr exposure and flaring of gills occurred after another 15–30 min. At that time the fish were returned to fresh water for 24 hr but did not recover.

Range of Lethal Dose at 4° C

Data presented in Table III indicate that the range of lethal dose was very close to the one observed at 11–11.5° C (Table II), although there is an indication that the fish were a little more sensitive to the lethal action of the drug at 4° C than at 11° C.

DISCUSSION

The sigmoid dose–response curve (Fig. 1) is typical of a system which records all-or-none response (Drill, 1954). The effective dose$_{50}$ (ED_{50})[3] as calculated from this curve is 43 ml/100 gal of water at a water temperature of 11–11.5° C. At 4° C while the spontaneous activity of fish was reduced by the lower temperature in absence of the anaesthetic the fish actively evaded attempts to capture them. At this temperature, however, the concentration of 2-phenoxyethanol required to produce anaesthesia was greatly reduced. A concentration which produced anaesthesia in only about 3% of fish (Fig. 1) at 11–11.5° C (30 ml/100 gal of water) produced 100% response at 4° C. ED_{50}, although not precisely determined at 4° C, would be in the vicinity of 25 ml/100 gal of water, on the basis of the data presented in Table I. This is considerably lower than the ED_{50} at 11–11.5° C. It should also be noted that the concentration of 25 ml/100 gal of water at 11–11.5° C produced anaesthesia in only 37% of the fish. This evidence indicates that the effects of 2-phenoxyethanol are potentiated as the water temperature is lowered (Goodman and Gilman, 1955).

The data for the determination of lethal dose$_{50}$ (LD_{50}) were too limited to permit an accurate estimation. However, this was not the objective of this study. It was intended to determine only an approximate range of lethal dose and from it to calculate an approximate LD_{50}. Since none of the fish exposed to the concentration of 130 ml/100 gal died and all of the fish exposed to 145 ml at 11–11.5° C died, it is reasonable to assume that the lethal range of dose is somewhere between 130 and 145 ml/100 gal of water. These results are in agreement with those reported by other workers (van Duijn, 1956). LD_{50} must, therefore, be higher than 130 ml/100 gal of water. Based on these figures the therapeutic

[3]ED_{50} is that dose of a drug which elicits a desired response in 50% of the animals exposed to it (Drill, 1954).

TABLE I. Response of sockeye salmon exposed to low concentrations of 2-phenoxyethanol in water at 4° C.

2-Phenoxyethanol[a] (ml/100 gal of water)	Fish in a batch	Fish responding	Fish responding
	no.	*no.*	%
15	4	0	0
20	5	0	0
22.5	4	2	50
	9	4	44
30	4	4	100
	4	4	100
	8	8	100
	8	8	100

[a]2-Phenoxyethanol was added after the effects of cold, alone, had been observed for at least 1½ hr.

TABLE II. Mortality in sockeye salmon exposed to high concentrations of 2-phenoxyethanol at 11–11.5° C.

2-Phenoxyethanol (ml/100 gal of water)	Fish in a batch	Duration of exposure	Fish dead	No. of deaths (% of total)
	no.	*hr*	*no.*	
85	4	8	0	0
100	4	8	0	0
115	4	8	0	0
	4	8	0	0
130	4	2	0	0
	4	8	0	0
	4	8	0	0
145	4	2	4	100

TABLE III. Mortality in sockeye salmon exposed to high concentrations of 2-phenoxyethanol at 4° C.

2-Phenoxyethanol (ml/100 gal of water)	Fish in a batch	Duration of exposure	Fish dead	No. of deaths (% of total)
	no.	*hr*	*no.*	
85	4	8	0	0
100	4	8	0	0
115	4	8	0	0
130	4	8	2	50
145	4	6	4	100

ratio $\left(\frac{LD_{50}}{ED_{50}}\right)$ of more than 3 is obtained. This ratio is high and indicates a large margin of safety (Goodman and Gilman, 1955) in the use of 2-phenoxyethanol as an anaesthetic in sockeye salmon.

At a water temperature of 4° C, ED_{50} was approximately 25 ml/100 gal of water (Table I), while LD_{50} was approximately 130 ml/100 gal of water (Table III) and the therapeutic ratio was thus greater than 5. This value is higher than that determined at 11–11.5° C. This would suggest that the margin of safety is increased when 2-phenoxyethanol is used at lower water temperatures.

No ill effects were observed with these fish during either their prolonged exposure (up to 12 hr) at 4° C or following their recovery in fresh water. Brett (1952) reported the lower lethal temperature for juvenile sockeye acclimated to 10° C was 2–3° C with 3 days exposure. Since the concentration of 2-phenoxyethanol required to anaesthetize the fish at this temperature is considerably less than that needed at higher temperature, it may be advantageous to use small doses of 2-phenoxyethanol in conjunction with lower water temperature, particularly when the fish are required to be anaesthetized for long periods of time.

In conclusion, it should be pointed out that the findings of this study may not be applicable, without modifications, to other species of fish. In mammals, well documented studies are available which show that apart from species differences several other factors can influence the response to a given dose of drugs. Some of these factors are weight (Rall and North, 1953), age (Dawson, 1940), sex and hormonal state (Holck and Mathieson, 1944) and environmental temperature (Chen and Anderson, 1943).

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Effects of Formalin on Length and Weight of Fishes[1]

By Robert R. Parker

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

Sockeye smolts, pink and chum fry, and pink and chum fingerlings (*Oncorhynchus*) were sequentially weighed and measured when alive and after death in water and after killing and storage in formalin up to 225 days. The fish shrank within 12 hours to 97% and by 30–40 days to 96% of live length. Further changes in length were not significant. These same relative changes were observed from fish of different sizes, and the values were not significantly different among groups preserved in formaldehyde solutions of fresh or sea water. In fresh water, fish gained weight while yet alive but under anaesthesia. In freshwater formalin, fish gained weight rapidly for 1 or 2 days, then lost weight at a decelerating rate to the time of last measurement. Fish killed and stored in salt water formalin lost weight for the first few days, then gained weight at a decelerating rate. Relative magnitudes and rates of change were inversely related to size of specimens contained in the sample. These changes had pronounced effects on relative condition factors which varied from 97 to 135% of live values depending upon size of fish, type of formalin and time in preservative.

INTRODUCTION

Preservation is known to affect both the length and the weight of fishes. For example, van Oosten (1929) reported that cisco (*Leucichthys artedi*) shrank both in length and weight when preserved in formalin and transferred to alcohol. Hile (1936) reported a similar shrinkage in length (loss of 1–2%). However, loss of weight was relatively greater (van Oosten, 4% loss; Hile, 15–17%) and individual changes were so varied that no standard correction factor seemed warranted. Shetter (1936) estimated that brook trout (*Salvelinus fontinalis*) within the total-length range of 2.75–10.125 inches shrank approximately 2.6% from *rigor mortis* alone. Shrinkage was approximately 5% from the live condition for brook trout preserved for 22–77 days in 10% formalin. A similar shrinkage was reported for brook trout fixed in formalin and stored in alcohol. Burgner (1962) reported shrinkages of sockeye smolts (*Oncorhynchus nerka*) preserved in 10% formalin ranging from 4.6 to 6.8% of live length, the larger percentages applying to the smaller fish (73–77 to 108–112 mm), in 5½ months. Approximately 80% of the total decrease occurred within the first 24 hours in preservative. Smolts shrank 2–3% in length due to *rigor mortis* alone.

Hoar (1939), utilizing the cube relationship to estimate condition factor, reported that formalin increased the apparent condition of Atlantic salmon (*Salmo salar*) parr and smolts. Specimens both shrank in length and increased in weight. Strength of solution affected the magnitude of change and differences were noted between the effects on parr and smolts. Clutter and Whitesel

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(1956) reported about 5% loss in length of sockeye smolts preserved in formalin. Original weights were not reported; however, a loss of 2% of weight occurred between 25 and 180 days. No differences in effect were detected due to strength of solution. Lux (1960) measured the average loss in length of yellowtail flounder (*Limanda ferruginea*) between live and landed condition (storage in ice) as 1.5%.

While these reported observations serve to alert the researcher to the problem that body dimensions are altered by various preservation media or death, no detailed time-sequence study appears available, and the variability between individuals in a sample and between samples is not explained. It is the purpose of this communication to present the results of a series of observations on the effect of formalin on the length and weight of juvenile sockeye, chum salmon (*O. keta*) and pink salmon (*O. gorbuscha*).

MATERIALS AND METHODS

Sockeye smolts were obtained from counting fences, either at lake outlets in the vicinity of the Kitoi Bay Research Station, Alaska, or at the Port John Field Station (Hooknose Creek), British Columbia. Pink and chum fry were obtained at the Hooknose Creek fence and pink and chum fingerlings were seined in the vicinity of Port John, approximately 2 miles (3.2 km) from the Hooknose Creek estuary. Live weights and lengths were observed for fish anaesthetized with Tricane-methane-sulfonate (MS. 222). The fish were then preserved by dropping them alive in a 3.8% solution of formaldehyde. Crowding was avoided to allow the specimens to assume a straight, fins-extended attitude during fixation. Lengths were recorded by laying the specimen on plastic-covered millimetre paper, nose at the zero line, and pricking a hole in the paper at the end of the middle rays of the caudal fin. Length measurements were rounded to the nearest whole millimetre. Weights were observed by blotting the specimen in damp towelling and weighing, in water, on a Mettler K7T balance. Weights were recorded to 0.01 g. Precision of these measurements will be discussed in following sections. Samples were stored in the original preservative in glass containers for the series of observations.

Because the present interest is in changes in weight and length and the resultant effects on relative condition factors (q) (Le Cren, 1951) and the exponent (y) of the allometric equation, $w = ql^y$, co-variance analysis (Snedecor, 1946) was employed on logged data. Three-place logarithms were used throughout.

RESULTS

Precision of Weight and Length Measurements

Precision of weight measurements was evaluated in two ways. Firstly, the degree of removal of surface or excess liquid is the most obvious source of error. A sockeye smolt, preserved in formalin for several months, was weighed after each of the following treatments: (1) *drip* — water was drained by touching the nose to damp towelling but not blotting; (2) *light* — blotting by rolling the fish once over damp towelling; and (3) *heavy* — rolling the fish over damp towelling

and applying light blotting pressure. The procedure was repeated seven times in each case. Results are presented in Table I. The greatest difference between adjacent treatments, as reflected by the means, was between drip and light, i.e. 0.149 g. Between light and heavy the difference was 0.070 g. Within each treatment, however, the standard deviations are quite small, demonstrating that a standardized method of blotting can yield reproducible results. The procedure labelled *heavy* is that adopted for the present study.

TABLE I. Weights resulting from repeated blotting procedures, sockeye smolt.

Test	Treatment		
	Drip	Light blotting	Heavy blotting
	g	g	g
1	5.39	5.30	5.17
2	5.36	5.24	5.18
3	5.38	5.22	5.15
4	5.39	5.21	5.18
5	5.38	5.21	5.18
6	5.38	5.24	5.17
7	5.40	5.22	5.12
Mean	5.383	5.234	5.164
s	0.0129	0.0316	0.0224

Further series of consecutive measurements were made to determine the error associated with weighing using the standard blotting procedure. Five separate sockeye smolts were used as follows: (a) preserved in formalin 11 months, 30 sequential weighings at 1-min intervals; (b) as in (a) except 28 sequential weighings; (c) as in (b); (d) in formalin 48 hr, 30 sequential weighings at 5-min intervals; and (e) in formalin 28 hr, 28 sequential weighings, 1-min intervals. Results are plotted in Fig. 1. In series a, b and c the weights appear to be distributed about a mean with no obvious trend. In series (d) and (e) consecutive weights appear to form declining trends. These trends must represent a progressive loss of water from those fish held in formalin 28 and 48 hr. This loss might have been caused either by the action of the formalin or by the previous weighing. Having no justification for the use of any particular curve, these data were fitted to second-degree polynomials and variance taken from the trend line rather than the means. Regression equations and standard deviations are given in Table II.

Variation in the amount of excess moisture removed before weighing undoubtedly contributed a major portion of the error noted as deviations from the base lines. Absolute error must, then, be partially related to the size of the fish, i.e. increasing as a function of the surface. Expressed as a percentage

of weight, the relative error may be expected to decrease as the size of the fish increases, i.e. those samples involving smaller fish will be marked by larger departures from an average or trend line. From the observations considered to this point, changes involving > 1.2% of the weight would be considered to

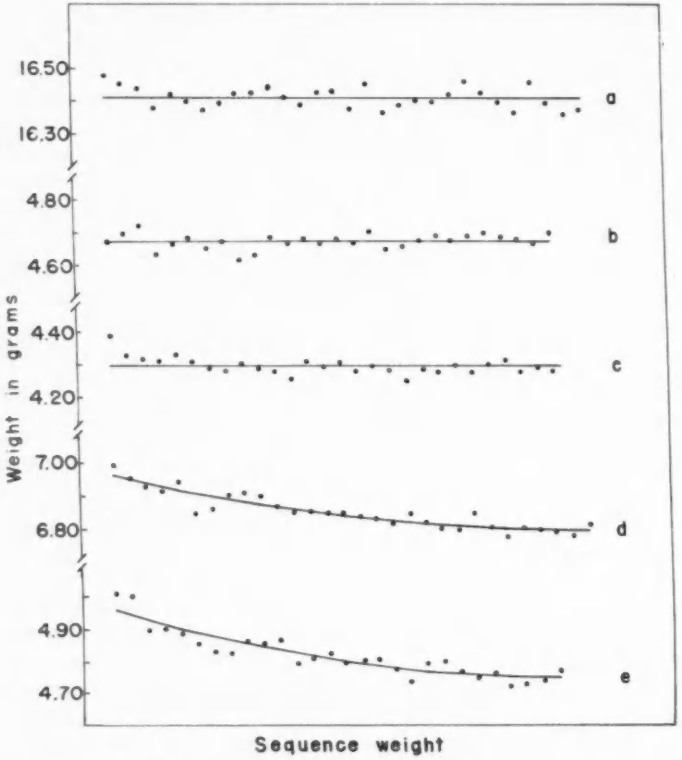

FIG. 1. Sequential series of weights taken of formalin-preserved sockeye smolts. Series "d" taken at 5-min intervals, remainder at 1-min intervals.

TABLE II. Sequential weighings for measurement of experimental error.

Sequence	Interval	Base line	Standard deviation
	min		
a	1	$w = 16.411$	0.031
b	1	$w = 4.674$	0.023
c	1	$\bar{w} = 4.298$	0.026
d	5	$\hat{w} = 6.970 - 0.0113t + 0.0002t^2$	0.021
e	1	$\hat{w} = 4.978 - 0.0164t + 0.0003t^2$	0.030

indicate real changes in the weight of the fish whereas changes involving less than these amounts may reflect experimental error. When smaller fish are weighed the relative error will be larger and vice versa.

Precision of length measurements was tested by sequential measurements on several fish. Rounding lengths to the nearest millimetre yields reproducible results; all measurements were within the interval $l \pm 1$ mm.

Changes Associated with Anaesthesia and Death

Five sockeye were used to observe fluctuations in weight occurring during prolonged anaesthesia and after cessation of respiratory movement, referred to here as "death". For each series, fish held in a 10-quart (11.5-l) container supplied with running water were removed and placed in a solution of anaesthetic until voluntary movement ceased. Surface water was then removed as described, the fish weighed in water, and returned to the original container. In two of the series (a and b) the sequence was timed to weigh at 10-min intervals; in the remaining (c, d and e) weights were taken at 5-min intervals but only the 10-min weights were used in the treatment of these data. Each series was continued for at least 5 hr. Each sequence of weights was first smoothed by a moving average of three and the resulting averages then expressed as percentages of the first average weight. The original average weights of each fish are as follows: (a) 4.26 g, (b) 4.90 g, (c) 18.92 g, (d) 26.71 g, and (e) 39.39 g. Results are graphically presented in Fig. 2. Time of death is indicated for each fish as an open circle.

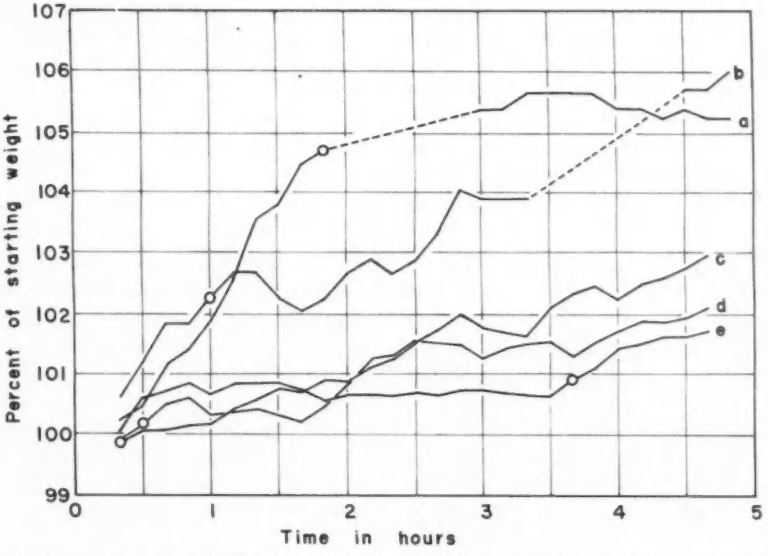

Fig. 2. Sequential series of weights of sockeye smolts taken during prolonged anaesthesia and death, smoothed by a moving average of 3 and expressed as percentages of the initial average value. Initial average values are: (a) 4.26 g, (b) 4.90 g, (c) 18.92 g, (d) 26.71 g, (e) 39.39 g.

Several features are of particular interest:

(1) In the two smaller fish (a and b), osmoregulation apparently was impaired after the first 30 min but prior to death. This resulted in a rapid uptake of water, hence, a gain in weight in fish (a) of about 4.8% and in fish (b) 2.2% prior to death.

(2) In fish (e) (the largest) respiratory movement continued, as did osmoregulation, for 3 hr, 40 min. During this time fluctuations in weight were relatively small but nevertheless real. It is not known whether these fluctuations reflect a normal cycle of water gain and loss or were induced by the treatment.

(3) The relative rate of water uptake was greater for small fish than for large fish.

It may be concluded that the live weight of a fish is affected by the particular stage of osmoregulation at the time of weighing, that osmoregulation is affected by prolonged anaesthesia and that the relative rate of water uptake is related to the size of the fish. If fish are weighed as soon as voluntary movement has ceased, live weight may be estimated within 1–2%.

Changes Occurring in Formalin

Two samples of sockeye smolts, obtained at the Hooknose Creek fence on April 27 and 28, 1961, were weighed and measured alive and preserved in a 3.8% solution of formaldehyde in fresh water. Each sample, designated as A (n = 102) and B (n = 88), respectively, was selected from smolts available to provide a wide range in size and does not represent the size frequency of the run. Comparison between the live length–weight relationships disclosed no significant differences between either the slopes (F = 0.69, d.f. = 1 and 186) or relative positions[2] (F = 0.02, d.f. = 1 and 187).

It is therefore concluded that these 2 samples may be considered as representative of the same population length–weight relationship.

Changes in length and weight occurring during storage in formalin are presented as a time series of geometric mean values in Table III. Co-variance tests indicated no significant differences between slopes obtained within each series (A:F = 1.75, d.f. = 10 and 1100; B:F = 1.87, d.f. = 9 and 860). Relatively large and significant changes in length, weight and relative condition occurred and these are expressed as a percentage of the live values in the last 3 columns of Table III.

Samples (n = 50) of pink and chum fry were taken at the Hooknose Creek fence on April 30, 1961, weighed and measured alive, and preserved in a 3.8% solution of formaldehyde in fresh water. Changes in length and weight during storage in the formalin are presented in Table IV. A co-variance test disclosed no significant differences among the slopes (pinks:F = 1.25, d.f. = 9 and 480; chums:F = 0.45, d.f. = 9 and 480). Changes in length and weight were relatively large and statistically significant.

[2]The term "relative position" refers to the relative height of the regression lines; i.e. if the slopes are not significantly different, do the lines coincide or do they lie at different elevations at a common length?

TABLE III. Changes in geometric means of length and weight, and relative condition factor (q), of Hooknose Creek sockeye smolts during storage in freshwater formalin.

Days in formalin	Geometric means		Per cent of live value		
	Length	Weight	Length	Weight	q
	cm	*g*			
Sample A (n = 102)					
0	10.85	9.65	...	...	...
0.8	10.46	11.26	96.4	116.7	130.6
1.8	10.48	11.18	96.6	115.9	128.8
3.8	10.53	11.03	97.0	114.3	125.3
5.8	10.51	11.00	96.8	114.0	125.9
7.8	10.56	10.70	97.3	110.9	120.8
14.8	10.51	10.70	96.8	110.9	122.5
17.7	10.58	10.73	97.5	111.2	120.2
34.8	10.11	10.90	95.9	113.0	128.2
103.8	10.39	10.83	95.7	112.2	128.5
224.8	10.41	10.65	95.9	110.4	125.3
Sample B (n = 88)					
0	9.34	6.06	...	...	...
1	9.06	7.28	97.0	120.0	131.5
3	9.13	7.11	97.7	117.2	125.9
5	9.13	7.07	97.7	116.6	125.3
7	9.10	7.04	97.4	116.1	128.2
14	9.15	7.06	98.0	116.4	124.2
22	9.17	6.88	98.2	113.5	120.2
34	9.02	6.91	96.6	114.0	126.8
103	9.00	6.87	96.4	113.2	126.8
220	9.04	6.71	96.8	110.7	122.2

Samples of pink (n = 182) and chum (n = 15) fingerlings were obtained offshore from Matthew Island, near Hooknose Creek, on May 14, 1961. These were transported alive to the laboratory and weighed and measured under anaesthesia. Formalin preservative was made up with sea water to a concentration of 3.8% formaldehyde. Sea water used was approximately 23‰ salinity. Changes in the geometric means of length and weight and changes in geometric means and relative condition, expressed as percentages of live values, are presented in Table V. Changes in slope were again not statistically significant (pinks:F = 1.35, d.f. = 8 and 1602; chums:F = 1.80, d.f. = 8 and 117).

Relative changes in length, weight and condition factor, as presented in Tables III, IV and V, are plotted as functions of time in Fig. 3, 4 and 5. The time scale (abscissa) is compressed and broken after 10 days to facilitate presentation, thus the apparent slopes have no direct meaning.

From the previous estimates of error in weighing (Table II), and using a sample size of $n = 25$, the standard error (S.E.) of the mean is estimated as approximately 0.005 g. Using the commonly accepted interval of ±2 S.E., true means are expected to lie within the interval $\bar{w}_G \pm 0.01$ g. In all cases except the Matthew Island chums, sample size was considerably larger than 25, and this estimate of S.E. is, therefore, a maximum. The interval $l \pm 0.1$ cm may be taken as a maximum estimate of 2 S.E. of l_G. Geometric means of live length and weight and confidence intervals of 2 S.E., expressed as percentages of the means, are presented in Table VI. Observed changes in the geometric means of length and weight cannot be accounted for as sampling error.

Fish shortened soon after they were put in formalin to about 97% of the original length. Length continued to diminish, slowly, to about 96% at around 30–40 days and stabilized at that level. Differences between size of fish, species, or type of formalin solution were not significant. Fluctuations about the obvious

TABLE IV. Changes in geometric means of length and weight, and relative condition factor (q), of Hooknose Creek pink and chum fry during storage in freshwater formalin.

Days in formalin	Geometric means		Per cent of live value		
	Length	Weight	Length	Weight	q
	cm	g			
Pinks ($n = 50$)					
0	3.42	0.202	...	...	...
1.2	3.33	0.253	97.2	124.9	133.3
2.0	3.33	0.257	97.3	126.8	135.3
3.9	3.34	0.256	97.6	126.3	133.7
5.9	3.31	0.248	96.8	122.4	132.0
7.9	3.28	0.246	95.9	121.6	134.1
14.9	3.30	0.230	96.4	113.7	123.7
44.9	3.25	0.225	94.9	111.2	125.8
96.0	3.25	0.216	95.0	106.7	120.3
217.9	3.27	0.213	95.6	105.5	117.1
Chums ($n = 50$)					
0	3.72	0.285	...	...	...
1.2	3.66	0.352	98.2	123.2	128.1
2.1	3.62	0.347	97.1	121.7	129.5
4.0	3.63	0.344	97.6	120.6	127.1
6.0	3.54	0.344	95.2	120.7	134.9
8.4	3.68	0.337	98.8	118.0	121.0
15.0	3.65	0.328	98.1	115.0	119.9
45.0	3.57	0.323	95.8	113.2	123.9
95.0	3.56	0.304	95.6	106.7	117.5
218.0	3.57	0.298	95.8	104.5	114.5

TABLE V. Changes in geometric means of length and weight, and relative condition factor (q), of Matthew Island pink and chum fingerlings occurring during storage in sea-water formalin.

Days in formalin	Geometric means		Per cent of live value		
	Length	Weight	Length	Weight	q
	cm	*g*			
Pinks (n = 182)					
0	6.00	1.60	...	...	...
1	5.86	1.46	97.7	91.2	98.2
2	5.85	1.48	97.5	92.5	100.2
5	5.85	1.48	97.5	92.7	100.5
17	5.74	1.53	95.7	95.5	109.9
24	5.70	1.45	95.1	90.6	106.4
38	5.75	1.49	95.9	93.5	107.6
85	5.75	1.53	95.9	95.9	109.4
205	5.77	1.52	96.2	95.1	107.6
Chums (n = 15)					
0	5.58	1.32	...	...	...
1	5.41	1.15	96.8	87.1	96.6
2	5.43	1.20	97.3	91.2	99.8
5	5.42	1.23	97.0	93.3	102.8
17	5.34	1.22	95.7	92.3	106.4
24	5.31	1.26	95.1	95.3	112.2
38	5.34	1.21	95.7	91.6	105.7
80	5.28	1.23	94.6	93.5	111.9
205	5.28	1.22	94.6	92.7	110.2

trend of mean lengths (Fig. 3), when compared with the magnitude of possible error given in Table VI, must be considered as of no significance.

Changes in weight, as depicted in Fig. 4, disclose differences between sizes, species and formalin solutions which are considered significant. In freshwater formalin, an initial period of rapid gain was followed by a protracted period of loss of weight. The magnitude of initial gain was inversely related to size of individuals making up the sample; however, a crossover occurred at about 30–40 days and smaller fish lost relatively more weight than larger ones. In salt-water formalin an initial short period of decreasing weight was followed by a protracted period of increase. The magnitude of change was also associated with size, although the changes were in an opposite direction to those occurring in freshwater formalin.

There are also fluctuations from apparent trend lines which appear significant. While a consistency in the subjective weighing method within any particular weighing period has been demonstrated, there may be differences between

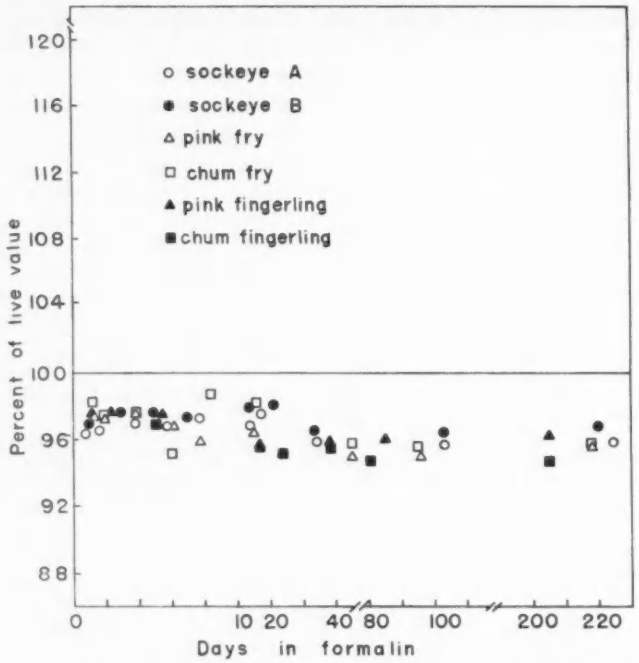

FIG. 3. Sequential series of geometric mean lengths of samples during storage in formalin, expressed as percentages of original live values. Sockeye smolts, pink and chum fry in freshwater formalin, pink and chum fingerling in sea-water formalin.

weighing periods. From those data presented in Table I it might be expected that such differences would amount to about 1.3% of mean weight for similar-sized fish. For any of the above series, fluctuations appear to be in the order of 2% or less and therefore may be largely or totally accounted for as errors in the weighing method.

Generalizing, average initial weight gains to 116–127% of original mean weight were observed for fish killed and stored in freshwater formalin. Weight subsequently fell to 105–111% of original live weight. The greatest relative gains and subsequent losses were associated with the smaller-sized fish. In salt-water formalin weight initially fell to 87–91% but subsequently rose to 91–95% of live weight. Again the larger relative changes are associated with the smaller fish. In spite of attempted precision in weighing, fluctuations of about 2% from the obvious trends occur and may be caused by error in the weighing method.

The effect of changes in length and weight on the relative condition factor (Fig. 5) reflects again the differences between the two types of preservative. In freshwater formalin initial increases to 128–135% were followed by decreases to 114–125% of original q. In salt-water formalin relative condition factors initially

TABLE VI. Geometric means of live length and weight and estimated 2 S.E. expressed as per cent of the mean.

Sample	$\bar{l}$ 2 S.E.	$\bar{w}$ 2 S.E.
	cm	*g*
Sockeye A	10.85 ± 0.9%	9.65 ± 0.1%
Sockeye B	9.34 ± 1.1%	6.06 ± 0.1%
Pink fry	3.42 ± 2.9%	0.20 ± 5.0%
Chum fry	3.72 ± 2.7%	0.28 ± 3.6%
Pink fingerling	6.00 ± 1.7%	1.60 ± 0.6%
Chum fingerling	5.58 ± 1.8%	1.32 ± 0.8%

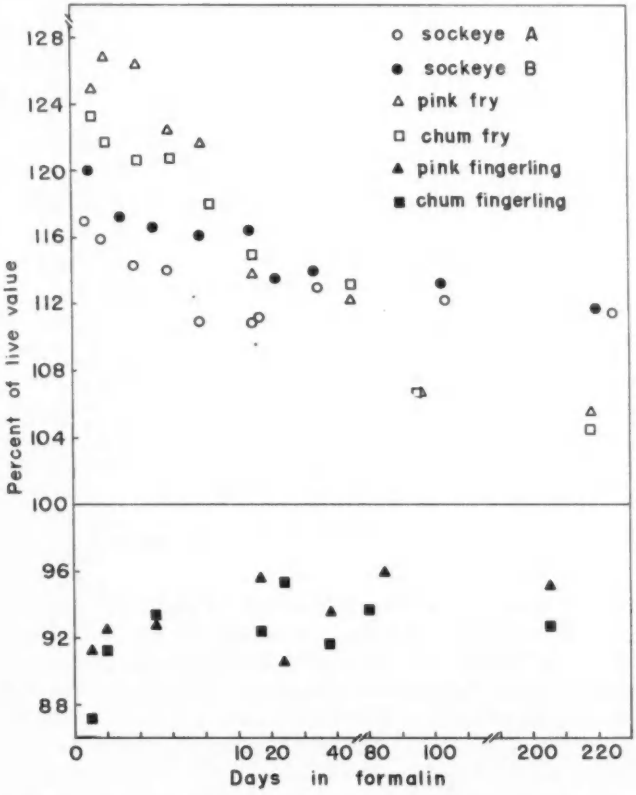

FIG. 4. Sequential series of geometric mean weights of samples during storage in formalin, expressed as percentages of original live values. Sockeye smolts, pink and chum fry in freshwater formalin, pink and chum fingerling in sea-water formalin.

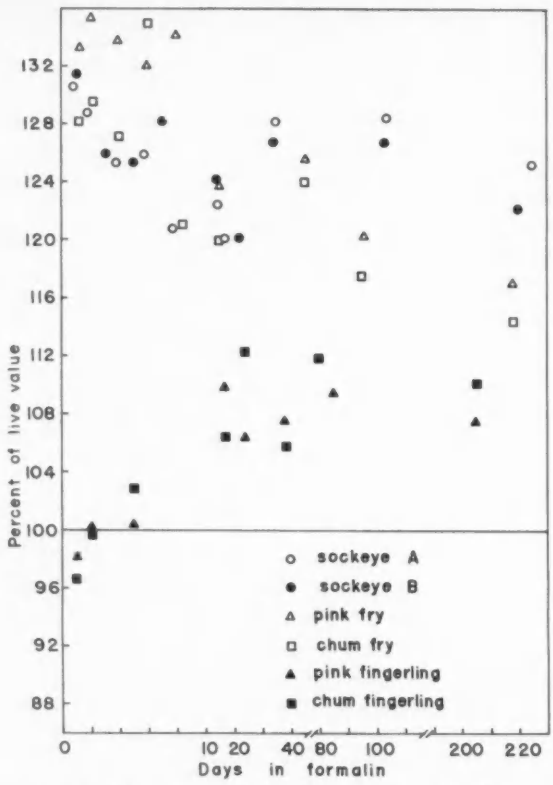

FIG. 5. Sequential series of condition factors of samples during storage in formalin, expressed as percentages of original live values. Sockeye smolts, pink and chum fry in freshwater formalin, pink and chum fingerling in sea-water formalin.

fell to 96–98% but subsequently rose to 107–110% of original q. It should be mentioned that errors in measurement become magnified in the relative condition factors and fluctuations from trend lines were in the order of 5% of q.

While relative changes in length were about the same regardless of size, relative changes in weight were greater in small fish than in large ones. It might be expected that the slopes of the length–weight regression lines within the series of any one sample would initially, in freshwater formalin, decrease and subsequently increase. The opposite effect would be expected in sea-water formalin. Co-variance tests for significance of differences between slopes have given, without exception, probabilities greater than 0.05. It is apparent, however, that differences between slopes approach significance at the 0.05 probability level when the samples contain fish falling into a sufficiently large number of length classifications. This feature may be observed in Table VII where the

F-ratios are compared with the ratio of longest to shortest fish within each sample. Values of the slopes are graphed as a function of time in Fig. 6. The initial decrease and subsequent rise in the slopes of the sockeye smolt series is obvious. Slopes of the pink and chum fry samples are relatively variable, but the pattern of initial decline and subsequent rise is nevertheless discernible. As expected, slopes of the pink and chum fingerling preserved in sea-water formalin reflect the opposite effect: an initial rise followed by a decline in y value. This analysis gives further evidence of the probable existence of a size effect on the effects of formalin on the length–weight relationship of fishes.

TABLE VII. Comparison of sample F-ratios for test of significance of differences among slopes with size ratios of longest to shortest fish in sample.

Sample	d.f.	F-ratio	$F_{.05}$	Size ratio[a]
Sockeye A	1100, 10	1.75	1.84	1.71
Sockeye B	860, 9	1.87	1.89	1.65
Pink fry	480, 9	1.25	1.90	1.16
Chum fry	480, 9	0.446	1.90	1.21
Pink fingerling	1602, 8	1.352	1.95	1.70
Chum fingerling	117, 8	1.796	2.02	1.45

[a]Longest fish in sample divided by the shortest.

DISCUSSION

The problem of gain or loss in weight is one of osmotic exchange of water and the amount of initial change (excluding the size effect) may largely depend upon the state of osmoregulation or amount of body water at the time of original measurement. The opposite reactions noted for formalin of different ionic strength dilutants confirm these views. The initial reactions and subsequent partial return toward live weights undoubtedly reflect chemical changes brought about by the preservative, which alter the osmotic strengths of fluids within the body and within the cells. In the present study a size effect has been noted which alters not only the relative amount but also the rate of water exchange. Changes have been recorded for only 225 days; continuation of the trends in time may be expected.

With the sources of error noted and the established variable effects of preservative solutions, it is difficult to evaluate many of the studies on condition factor reported in the literature. Such terms as "live weight" or "fresh condition" are not sufficiently descriptive to establish the degree of water uptake at the time of weighing. A freshwater fish which has been captive in a gill-net for 12 hr may be in a fresh condition but 120% of its live weight. Weights of fish held in water with insufficient oxygen or kept in water after death until weighing may not be equivalent to live weights or even a constant percentage of live weights. It is necessary that treatments be throughly described and unless these factors are standardized within any experiment, the comparison of results may simply reflect differences due to treatment rather than differences in the environment.

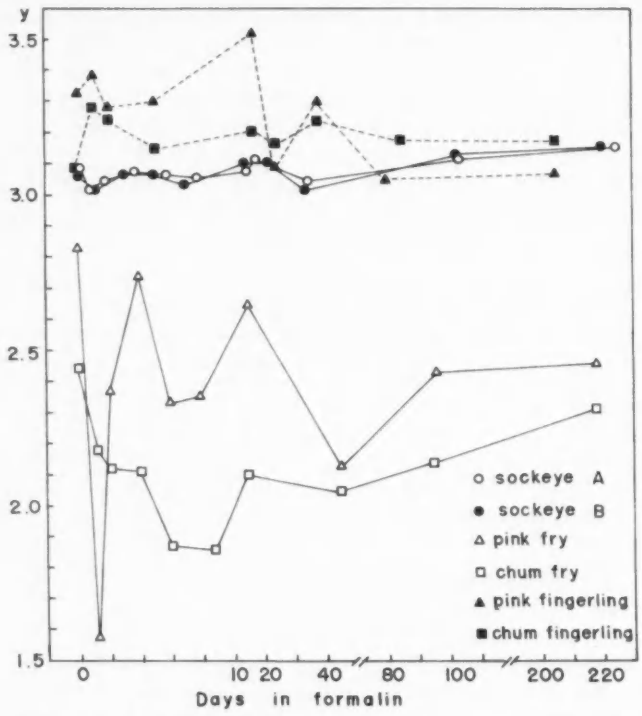

FIG. 6. Sequential series of values of slopes of $\log l \times \log w$ regression lines for samples stored in formalin. Sockeye smolts, pink and chum fry in freshwater formalin, pink and chum fingerling in sea-water formalin.

These observations appear to preclude the establishment of any usable generalized correction factor for the effects of formalin on weight. Rather, for each situation, correction factors should be carefully established taking into account original state and size of the specimens, strength of formaldehyde solution, ionic strength of dilutant, and time in preservative. It may be possible to adjust the preservative ionically so that weight will return to a value not significantly different from live weight. Such a technique undoubtedly will create its own problems of control.

SUMMARY

Changes in length were recorded by sequential measurements of fish killed and stored in 3.8% formaldehyde solution. Fish shrank to 97% of original length in less than 24 hr, and subsequently shrank to 96% of original length at 30–40 days. Further changes were not considered significant. Ionic strength of solution or size of fish were not observed to influence the relative magnitude of change.

Changes in weight were recorded during anaesthesia and after death in water for as long as 5 hr. It was concluded that, for fish under anaesthesia, weight must be observed as soon as voluntary movement ceases in order to approximate live weight within 1 or 2%. Prolonged anaesthesia, although respiratory movement may continue, and death affect osmoregulation.

In freshwater formalin weight increased rapidly during the first 1 or 2 days then decreased at a decelerating rate, approaching 105–112% of live weight at 205–225 days. The relative magnitude and rate of initial gain and subsequent decline was inversely related to the size of fish in the sample. Opposite effects were observed for fish stored in formalin made up with 23‰ salinity sea water. These changes caused relative condition factor to vary from 97 to 135% of live value depending upon the type of formalin solution, size of the fish, and time in solution. Size differences affected the slopes of $\log l \times \log w$ regression lines. It was concluded that no standard correction terms would be generally usable; correction terms would have to be determined for each study taking into account the original state and size of fish, ionic concentration of the formalin and the time in the preservative.

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Olfactory Perception in Migrating Salmon
III. Stimulants for Adult Sockeye Salmon (*Oncorhynchus nerka*) in Home Stream Waters[1]

By U. H. M. Fagerlund, J. R. McBride, M. Smith and N. Tomlinson

Fisheries Research Board of Canada
Technological Research Laboratory, Vancouver, B.C.

ABSTRACT

Adult sockeye salmon (*Oncorhynchus nerka*) captured during their spawning migration to Great Central Lake, British Columbia, show a consistent response in the laboratory to water taken from the outlet of the lake. The specificity of this response has been confirmed and the responses to water from streams feeding Great Central Lake have been determined. A portion at least of the stimulatory material is volatile and can be retained in a cold trap. Concentration of the active factor has been achieved by a freezing-out technique.

INTRODUCTION

The extreme sensitivity of the olfactory receptors in fishes and the importance of odour cues in their behaviour is well established (e.g. Hasler, 1957, 1960a, b; Beidler, 1961; Creutzberg, 1961; Pfeiffer, 1962). Buckland, in 1880, postulated that the migrating adult Atlantic salmon (*Salmo salar*) locates its spawning ground by smell. Experimental evidence in support of this theory, as applied to the later freshwater stages of spawning migrations, is provided by the studies of Wisby and Hasler (1954) and of Collins *et al.* (1962) on two species of Pacific salmon (*Oncorhynchus kisutch* and *O. tshawytscha*). Recently, a response of sockeye salmon (*O. nerka*) to their home stream water has been demonstrated in a laboratory bioassay (Idler *et al.*, 1961). The present paper is concerned with experiments aimed at the characterization of the home stream stimulant for sockeye salmon migrating into Great Central Lake, Vancouver Island, British Columbia.

METHODS AND PROCEDURES

Experiments were carried out during the spawning migration of 1961 and 1962. Fish migrating into Cultus Lake, British Columbia, were studied for comparative purposes in 1961. Methods employed in the capture and transport of adult *O. nerka*, and routine aquarium procedures have been described (Idler *et al.*, 1961; McBride *et al.*, 1963; Sehdev *et al.*, 1963).

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Assay Procedures

Bioassay procedures were essentially identical to those used previously (Idler *et al.*, 1961) with one modification. This modification entailed the injection of dechlorinated supply water into the assay system during the control period immediately before each assay. This modification was instituted when it was realized that the fish would occasionally show unexpected response behaviour (see below). When a response occurred during the control period, testing was abandoned until the fish again became quiet. A group of four healthy female fish was utilized in the assay. The fish were discarded after 10–15 assays. Usually male fish were not used as they were much too active.

The intensity of the response is recorded in the Tables by the use of numerals. No response at all, indicated by 0, corresponded to the control condition. In this condition, the four fish remained quiet in the shaded area of the assay tank (Idler *et al.*, 1961) making only occasional circling movements. A weak response, indicated by 1, was one in which some increase in activity in the shaded area of the tank occurred, coupled with occasional excursions into the lighted area. A strong response, 2, was characterized by a marked increase in activity, and the entry of at least three fish into the lighted area.

In some instances the activity of the fish appeared to take the form of an attempt to escape, the fish moving up and down one side of the tank with their noses pressed against the wall or jumping out of the water. Home stream water in an amount less than half that required to produce a full response seldom evoked even a weak one.

Home Stream Water

Previously described procedures (Idler *et al.*, 1961) were followed in collection and transport of water samples. Polyethylene bottles (20 l) were employed for collection and storage (at 0°) of some samples.

Concentration of Home Stream Stimulant

Two techniques were investigated. The first involved partial freezing of water samples by methods essentially the same as those described by Shapiro (1961). The second involved passing a stream of nitrogen gas through the water at 25°. The volatile components carried off were trapped by passing the emerging gas through two 2-l glass-wool-packed spherical containers in succession, the containers being rotated in a dry ice–acetone bath. After the aeration was completed, the trapped contents were rinsed out with cold, distilled water. A flow rate of 300 ml of nitrogen per min through 20 l of water was maintained.

RESULTS

Specificity of Response to Home Stream Water

The combined data for 1960 and 1961, demonstrating the specificity of the response of Great Central Lake and Cultus Lake sockeye to water leaving these lakes is presented in Table I. It became apparent during 1961 that anomalous responses by the fish were occasionally encountered (see Great Central Lake fish

(in Table I). A bioassay such as the one employed in this investigation has a weakness in that it presupposes that the activity of the test fish will remain constant until it is changed through the influence of an external stimulus. While all obvious precautions have been taken to exclude unwanted external sources of stimulation, such as changes in water temperature (see below), variations in light and noise level, inexplicable changes in the activity of the fish have occasionally been observed, and such occurrences presumably account for the anomalous responses recorded. The nature of the response is such that it is perhaps not surprising that anomalous results should occasionally be encountered.

TABLE I. Specificity of response to home stream water.

Fish from	Water from	Response intensity and no. of tests		
		0	1	2
Great Central Lake	Great Central Lake	1	–	23
Great Central Lake	Cultus Lake	4	–	1
Cultus Lake	Cultus Lake	–	–	7
Cultus Lake	Great Central Lake	2	–	–

It has been found that a relatively large difference in temperature between the water under test and the aquarium water can stimulate a response in the fish (Table II), which at times is indistinguishable from that elicited by home stream water. In practice, of course, temperature differences of this magnitude are easily avoided. Fish in an advanced stage of sexual "ripening" respond erratically, and most of the fish used tend to become unresponsive to their home stream water following repeated testing.

TABLE II. Effect of temperature of test water on response.

Temp. °C		Response intensity and no. of tests		
Test Water	Tank Water	0	1	2
0.0	14.0	–	1	1
15.0–17.5	13.5–14.0	5	–	–
19.0–19.5	13.5	–	1	1

In spite of the anomalies mentioned, however, in the great majority of the tests carried out the fish have responded in a manner that indicates a response to water from their home stream and not to that from other sources.

Response to Water from Creeks Flowing into Great Central Lake

In the initial work with Great Central Lake fish (Idler *et al.*, 1961), their responses to waters from Forestry Camp, Lindsey and Drinkwater Creeks were investigated. Subsequently, additional experiments with these and other Great Central Lake tributaries have been carried out. The results of all experiments are recorded in Table III.

Table III. Response of Great Central Lake sockeye salmon to water from tributaries to that lake.

Tributary creek		Intensity of responses and no. of tests		
		0	1	2
Forestry Camp	1960	2	–	–
	1961	–	–	1
	1962	2	–	1
Lindsey	1960	–	–	2
	1962	–	3	2
Fawn Point	1961	–	1	–
McBride	1961	1	–	1
	1962	2	1	–
Drinkwater	1960	–	–	2
	1961	1	3	–

In each year the volume of water tested was the same as the volume of lake outlet water required for a strong response.

Response to Water Collected at Different Depths in Great Central Lake

Because the stimulant in Great Central Lake water is volatile (Idler *et al.*, 1961) there is a possibility of active material being lost from surface water. Therefore, water collected at the following depths and temperatures was tested: surface (18.5°); 10.5 m (18.0°); 12 m (14.0°); 18 m (9.5°). Except for one of three samples collected at 18 m, all appeared to be of equal strength, i.e. a minimum of 110 l was required for a strong response[2]. In the one exception, 70 l rather than 110 were found to be sufficient.

Concentration of Stimulant

A four- to eight-fold concentration of home stream attractant was achieved using the freezing-out technique. Typical experiments are detailed in Table IV.

[2]Testing of these samples was conducted in 1962, when 100 l of lake outlet water were required for a full response. In 1961, only 72 l were required.

The results achieved in the experiments where the stimulant was removed in a stream of nitrogen are summarized in Table V. Although not shown on this table, in one preliminary experiment the fish did not respond to the recombined volatile and non-volatile fractions presumably because of the inefficiency of the trapping system.

TABLE IV. Concentration of stimulant by freezing-out.

Experiment No.	Reduction in volume (litres)	Response intensity	
		Ice	Concentrate
1	144 to 72	1	2
2	72 to 9	1	2
3	180 to 27	–	2

TABLE V. Removal of stimulant from 72 l of lake water by nitrogen gas.

Experiment No.	N_2 passed (hours)	Response intensity		
		Water	Trap	Combined
1	3	0	1	–
2	6	0	1	–
3	5	–	–	2
4	6	–	–	2

DISCUSSION

The evidence presented above indicates that Great Central Lake sockeye salmon quite consistently respond to Great Central Lake water in the laboratory. The specificity of this response in the sense that Great Central Lake salmon do not respond to Cultus Lake water and vice versa has been confirmed.

The sockeye salmon entering Great Central Lake via Stamp River in early summer are "green" (Idler *et al.*, 1961; Schmidt and Idler, 1962). After 3 to 4 months spent in the lake, the fish spawn, in the main, on 3 gravel beaches at Lindsey Creek, Fawn Point and Forestry Camp (listed in decreasing order of importance) and, to a minor degree on Spring Creek Beach, and in Lindsey, Drinkwater and Taylor Pass Creeks (F. Boyd, personal communication). It is of interest that none of the waters in the creeks emptying on the main spawning beaches was as effective in stimulating the salmon as was the water collected at the outlet of the lake, except possibly for water from Lindsey Creek, the creek whose outlet is in the major spawning area, Lindsey Creek Beach. It is known that sockeye salmon home specifically to spawning areas in systems similar to Great Central Lake (Hartman and Raleigh, 1962), but it is not yet

known if sockeye in the Great Central system home in a similarly specific manner to their several spawning areas. The test fish were collected as they entered Great Central Lake and presumably fish bound for each spawning area are present in numbers proportional to their total population. The results recorded in Table III could be a reflection of this, assuming each spawning area has its own specific attractant.

The results of attempts to concentrate the stimulant indicate that at least a portion of the stimulatory material is volatile. However, the fact that recombined volatile and non-volatile fractions induced a stronger response than did the volatile alone, suggests that a non-volatile material may play some part in stimulating the fish.

In this connection it is interesting that the attractants from Wisconsin streams to which bluntnose minnows (*Thyborhynchus notatus*) respond after training (Hasler and Wisby, 1951) and the chemical attractant for the sea lamprey (*Petromyzon marinus*) present in teleosts (Kleerekoper, 1961, 1963) are also volatile. In contrast, neither the attractant for juvenile sockeye salmon (*O. nerka*) present in food (McBride *et al.*, 1962, and unpublished results) nor the repellent for salmon present in mammalian skin (Idler *et al.*, 1956) is volatile.

It has been mentioned above that responses in our bioassay system can be produced by factors other than those specific to home stream water. Investigation of one of these, temperature differences between test water and water in the assay tank (Table II), suggests that the minimum temperature difference needed to produce a response is 5–6°C. Since there was a twenty-fold dilution of the test water during assay, a sensitivity to differences of 0.25°C is implied, although there is a possibility of non-uniform mixing. Thus, the adult sockeye salmon must be at least as sensitive to temperature differences as are other species of fish (Bull, 1957).

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Fecundity of Grand Bank Haddock[1]

By V. M. Hodder

Fisheries Research Board of Canada
Biological Station, St. John's, Nfld.

ABSTRACT

The fecundity of Grand Bank haddock was investigated from 229 specimens collected during the early springs of 1957–61. It was found that fecundity increased at a rate proportional to about the fifth power of the body length and to the square of the age, the correlations between fecundity and length and between fecundity and weight being better than that between fecundity and age. Within any age-group fecundity was found to increase with length. Since the larger fish of an age-group are the first to mature, it is suggested that fecundity of individual fish may be more directly related to the number of times that the fish has spawned than to such parameters as length, weight or age. Certain differences in fecundity, found between the samples of the individual years, are discussed in relation to such environmental conditions as temperature in so far as it determines the degree of haddock concentration (thus affecting the food supply) at certain times which are probably critical during the early development and maturation of the ova.

INTRODUCTION

The only other comprehensive study of haddock fecundity is that for North Sea haddock by Raitt (1933), who recognized the serious effect that a high exploitation rate might have on the spawning potential of the stock once the age structure changes, so that the propagation of the species must depend on the egg production of much younger spawners. In the Northwest Atlantic the haddock (*Melanogrammus aeglefinus* (L.)) population on the Grand Bank has undergone intensive exploitation since 1947, and consequently the age structure has changed considerably. This is also aggravated by the great variation in year-class survival that has been apparent from the earliest years of the fishery. As a contribution to the knowledge of the general biology of the Grand Bank haddock stock, this paper presents information on the fecundity of haddock as it is related to such parameters as length, weight and age. During the course of the investigation great variation in the fecundity of individual fish of the same size and age was observed and differences from year to year were found. The significance of these results is discussed in relation to some factors affecting the environment.

MATERIALS AND METHODS

The material on which this paper is based was collected during the springs of 1957–61 and is listed in Table I. All specimens were taken from an area along the southwest slope of the Grand Bank (Fig. 1) where haddock are usually heavily concentrated during winter and spring. The 1957 and 1958 samples were obtained from the landings of commercial trawlers. Before examination

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TABLE I. Number of haddock ovaries sampled for fecundity estimation in each year with the date of capture and range of length and depth.

Year	Date	Depth range	Number of specimens	Length range
		fath		*cm*
1957	Mar. 28–31	60–90	42	38–63
1957	Apr. 2	51	50	39–64
1958	Apr. 9–15	48–52	23	39–53
1959	Apr. 30–May 12	47–148	46	38–59
1960	Apr. 30	42	52	36–54
1961	Mar. 8	95–105	16	39–54
			229	

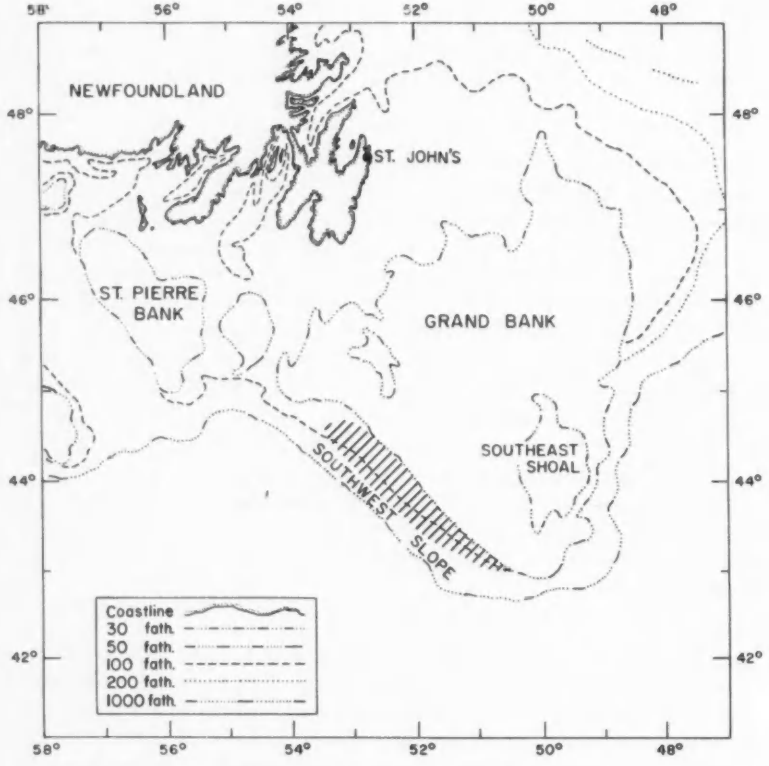

FIG. 1. Map of the Grand Bank showing the approximate location (diagonal hatching) of the winter and spring concentrations of haddock.

and removal of the ovaries in the laboratory these samples were preserved in ice on board ship for 2–5 days, but the ovaries were in excellent condition for fecundity estimations. All subsequent samples were obtained from the catches of the research trawler *A.T. Cameron* during the normal course of surveying the haddock concentrations in the area.

Mature haddock of the Grand Bank generally spawn during the months of May and June, but a few may spawn in late April and also in early July, the variation in average annual spawning time being largely related to hydrographic conditions throughout the area during the preceding months. The ovaries of mature female haddock, which are approaching the time of spawning, contain 3 types of eggs: (a) minute grey-coloured yolkless eggs less than 0.1 mm in diameter, (b) larger opaque yellow-coloured eggs 0.5–1.0 mm in diameter, and (c) still larger translucent eggs about 1.5 mm in diameter. Ovaries, examined a month or two subsequent to spawning, still contain the grey-coloured masses of minute eggs, but usually only a few of the larger opaque and translucent eggs are found. It would seem, therefore, that only the eggs of the last 2 types are involved in the immediate spawning, the first type being eggs which will develop for spawning in the following or subsequent years. Raitt (1933), in fecundity studies of North Sea haddock, has reviewed the previous literature and concluded that the minute yolkless eggs must not be considered in fecundity estimations. With a knowledge of the spawning time in mind, the present collections were made at times in the spring when most of the ovaries still contained opaque yolky eggs which were of such a size that they could be easily distinguished from the minute grey-coloured eggs. Ovaries which were so advanced as to contain large translucent eggs were not used in this investigation.

For each fish collected in 1957, 1958 and 1960, the fork length, whole weight, gutted weight (less gills) and weight of ovaries were recorded, and both otoliths and scales were taken for age determination. The 1959 and 1961 samples were collected at sea and no weights are available. The weights were initially taken in pounds, but kilogram equivalents have been used in this paper.

The ovaries from each fish were carefully removed, weighed to the nearest gram, slit longitudinally and placed in a bottle containing Gilson's fluid. The method of preservation was the same as that followed by Simpson (1951) for North Sea plaice, for which the normal solution was modified by doubling the amount of acetic acid. This solution not only preserved the eggs but broke down the intra-ovarian connective tissue. The process was aided by vigorously shaking the bottles several times during the next few days. The best results were obtained when the ovaries were removed from Gilson's fluid within 2–4 weeks after preservation, the external ovarian wall removed, and the egg clusters returned to bottles containing a fresh solution of Gilson's fluid for a few days during which the bottles were shaken periodically. Eggs left in Gilson's fluid for more than 2 or 3 months were found to be in poor condition and had to be discarded. When the complete ovaries were initially left in Gilson's fluid for too long a period, the outer ovarian wall had disintegrated so much that it was difficult to remove the pieces.

The eggs were cleaned by straining the contents of the bottle on a very fine-mesh nylon bolting cloth (70 meshes per inch) stretched loosely across the mouth of a large glass funnel. Any residual pieces of ovarian tissue were removed with forceps and the remaining egg clusters were broken down by spraying them with water through a small glass nozzle at the end of a length of flexible rubber tubing attached to the water supply. This procedure also facilitated the removal of most of the minute second-generation eggs, which passed through the meshes of the bolting cloth. The opaque yolky eggs were then transferred to a bottle containing a solution of 5% formalin, in which they were preserved until the fecundity estimations were made.

The apparatus used for the fractioning of the egg samples was a whirling vessel. A description of this vessel and its operation has been given by Wiborg (1951). The bottom part of the cylindrical container is divided radially into 10 compartments of equal size. When the egg sample is poured in with an adequate amount of water, the vessel rotated rapidly and suddenly stopped, the eggs become evenly distributed throughout the liquid in the container. They are left to settle at random in the compartments for a minute or two before the liquid is drained off through screened openings in the inner cylinder. The subsamples of eggs (1/10) can then be removed from the individual compartments by flushing them through holes which can be opened in the base of the outer cylinder. Two subsamples were generally taken, one to be further fractioned and the other to be kept in case the first was accidentally wasted. Repeated fractioning produced further subsamples, the number of successive fractions being dependent on the size of the ovary or the apparent quantity of eggs. The eggs of small ovaries were usually fractioned twice producing subsamples of 1/100, while for larger ovaries further fractionations or combinations of subsamples produced final subsamples of 1/500 and 1/1000. Two subsamples were generally taken for counting, but in a few cases 2 additional subsamples were taken when the first 2 produced quite different counts. In such cases all 4 counts were used for the fecundity estimate.

The subsample to be counted was placed in a petri dish, and by means of fine-pointed dissecting needles the ova were counted under the low power ($\times$ 5) of a binocular microscope. During the process of fractioning an effort was made to limit the size of the subsample to 1000–3000 ova. Most of the counts fell within this range, but some were as low as 500 and others as high as 7000 ova.

No attempt was made to test the reliability of the sampling technique, since the whirling vessel of the type used was tested by Wiborg (1951) and found to be quite reliable. However, some indication of the deviation of the egg samples from their mean for each specimen may be obtained by computing the percentage deviation from the mean for all cases in which 2 or more subsamples were counted to obtain a fecundity estimate. It will be noted from the frequency distribution of the percentage deviations (Table II) that 137 of the 180 observations deviated from their means by less than 10%.

TABLE II. Frequency of the percentage deviations from the mean fecundity for the ovaries for which 2 counts were made.

Range of percentage deviation	No. of specimens
0–4.9	83
5–9.9	54
10–14.9	26
15–19.9	12
20–24.5	4
25–29.5	1
	180

RESULTS

FECUNDITY RELATED TO LENGTH

Fecundity estimates were made for 229 Grand Bank haddock. From the scatter diagram of fecundity against body length (Fig. 2) it is apparent that fecundity increases at a rate greater than the length of the fish. Assuming that growth in form is isometric, it would be expected that the relationship between fecundity and length is of the cubic form. The present data may be tested for this possibility by computing for each length interval the value of F/L^3, where F is the arithmetic mean fecundity estimate and L the mid-point of the length interval. These calculations for the data of the 5 years separately and together are given in the first part of Table III. The values of F/L^3 show a definite tendency to increase with size, indicating that fecundity increases at a rate greater than the cube of the length.

A logarithmic transformation was next applied to the 2 variables, and the relationship between log fecundity and log length expressed in the form

$$\log F = n \log L + \log k.$$

The resulting fecundity–length curve for the data of all years combined is shown in Fig. 2. The regression coefficients n and intercept values $\log k$ for the separate and the combined data are given in Table IV together with the corresponding correlation coefficients r. Except for the data of 1958 and 1961, for which the number of observations are small, the fecundity–length relationships indicate that fecundity of Grand Bank haddock increases at a rate close to the fifth power of the length.

The data of Fig. 2 also indicate that for any one length of fish the fecundity varies between wide limits. This variation is much greater than would be expected due to sampling errors and tends to mask any annual differences in fecundity that otherwise might be apparent. This aspect, however, is better shown by comparing the geometric means of the fecundity-at-length data with the values taken from the fitted log–log regression (Table III). The data of

TABLE III. Ratios of fecundity to length cubed, and the geometric mean fecundities by length and year of capture for female haddock of the Grand Bank, 1957–61.

Length 2-cm intervals	Fecundity/length³						Geometric mean fecundities in thousands of ova (figures in parentheses are numbers of specimens)						Range of estimates ('000)	Fecundity calculated from curve ('000)
	1957	1958	1959	1960	1961	1957–61	1957	1958	1959	1960	1961	1957–61		
36–37	...	...	...	2.82	...	2.82	...	...	...	137(2)	...	137(2)	131– 144	134
38–39	3.10	3.24	2.28	3.26	2.51	2.96	152(5)	176(2)	127(2)	143(3)	138(2)	148(14)	48– 320	176
40–41	3.22	4.67	2.75	...	...	3.25	211(6)	310(3)	175(9)	...	...	205(18)	95– 380	228
42–43	4.60	4.82	2.61	5.07	6.72	4.26	306(10)	327(5)	190(12)	363(8)	450(3)	284(38)	101– 909	292
44–45	5.21	6.41	3.51	5.44	4.77	5.13	415(10)	543(4)	290(6)	460(17)	375(4)	418(41)	146–1044	369
46–47	5.51	3.97	3.90	6.86	4.82	5.39	524(21)	381(5)	360(8)	666(12)	484(2)	504(48)	148– 963	462
48–49	4.94	2.61	5.38	6.51	4.56	5.14	521(16)	298(1)	600(3)	727(4)	520(1)	546(25)	205–1156	572
50–51	6.65	4.12	...	5.07	3.59	5.63	814(8)	520(2)	...	647(2)	456(2)	680(14)	388–1500	704
52–53	5.08	6.43	4.73	6.92	...	5.41	713(4)	931(1)	660(4)	1002(2)	...	755(11)	455–1041	859
54–55	7.20	...	5.56	5.15	5.47	5.89	1100(2)	...	900(1)	834(2)	846(2)	916(7)	621–1551	1040
56–57	7.11	...	...	...	...	7.11	1269(4)	...	...	...	...	1269(4)	1085–1616	1248
58–59	6.86	...	6.07	...	...	6.60	1357(2)	...	1216(1)	...	...	1308(3)	1216–1588	1493
60–61	6.63	...	...	...	...	6.63	1422(2)	...	...	...	...	1422(2)	1102–1834	1773
62–63	7.16	...	...	...	...	7.16	1748(1)	...	...	...	...	1748(1)	...	2093
64–65	8.04	...	...	...	...	8.04	2158(1)	...	...	...	...	2158(1)	...	2460

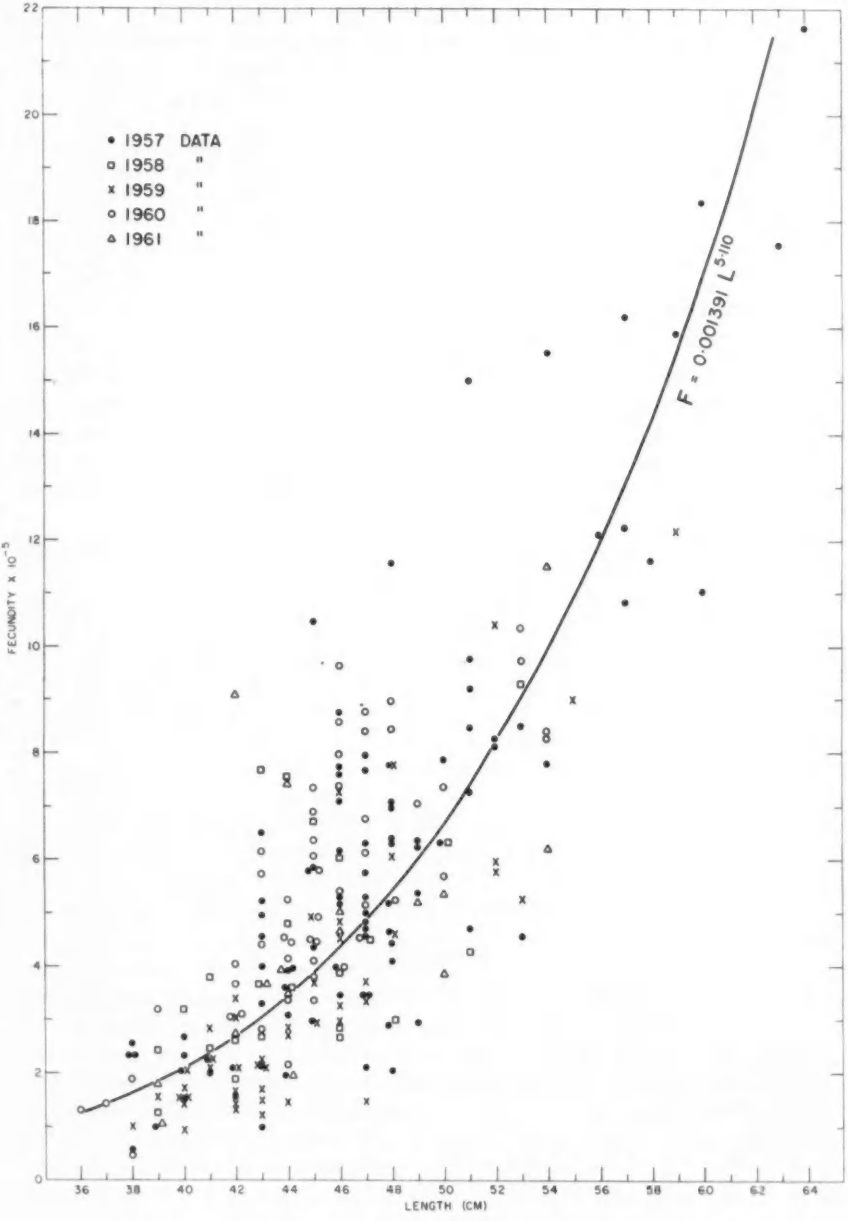

FIG. 2. Fecundity estimates for Grand Bank haddock by length and year of capture together with the fitted regression line.

TABLE IV. The relationships between log fecundity and log body length for the samples of 1957 to 1961.

Year	No. of fish	Regression coefficient, n	Intercept log k	Correlation coefficient, r
1957	92	4.913	−2.5189	0.81
1958	23	3.635	−0.4098	0.60
1959	46	5.724	−3.9843	0.88
1960	52	5.515	−3.4423	0.80
1961	16	4.143	−1.2525	0.67
1957–61	229	5.110	−2.8566	0.79
1957–61 (omitting 1959)	183	4.773	−2.2664	0.79

1957, being the more substantial, follow closely the fitted curve. The 1958 data are quite irregular for haddock between 44 and 51 cm, but only 23 observations were made in that year. The 1959 data follow closely the shape of the fitted curve but are consistently below it throughout its entire length. The 1960 fecundity averages are in most instances above the fitted curve, while those for 1961 are irregular, being based on only 16 fish.

In order to test the significance of the between-yearly differences in intercept (log fecundity adjusted to a common log body length), and in slope (rate of increase of log fecundity with log length), an analysis of covariance was used according to Snedecor (1956). The F-value derived from the ratio of mean square for adjusted means to mean square for common regression measures the significance of the sample differences in intercept. The F-value derived from the ratio of mean square for regression coefficients to mean square within samples measures the degree of variability in the regression coefficients or slopes.

No significant difference was found between the regression coefficients of the yearly samples ($F = 1.20$; $F_{.05} = 2.41$), but a significant difference at the 1% level resulted when the test was applied to measure the variability in intercepts ($F = 9.33$; $F_{.01} = 3.41$). It has already been noted that the fecundity averages for 1959 lie below the fitted curve. In an analysis of covariance of the data, omitting the fecundity estimates for 1959, neither the regression coefficients nor the intercepts are significantly different at the 5% level. Similar tests were applied by omitting the data of 1958, 1960 and 1961 individually, but the results were essentially the same as those in the first test. Consequently the variation shown by the first test is due in large part to the inclusion of the 1959 data.

The only other known fecundity estimates for Grand Bank haddock are those of Rojo (1956). He examined 19 specimens caught in 1955 and showed the mean fecundities by 3-cm length intervals on a graph. The number of observations at each length interval is not given, nor does he mention his sampling techniques. In Table V are given Rojo's estimates as taken from a graph and, for comparison, the present data grouped by 3-cm intervals. Rojo's fecundity estimates, particularly at the larger sizes, are not much more than half of those obtained from the present 1957–61 data.

TABLE V. Comparison of mean fecundity estimates of Rojo's 1955 data for Grand Bank haddock with those of the author's 1957–61 data (number of observations in parentheses).

Length interval (3-cm)	Mean fecundity estimates	
	Rojo's 1955 data	Present 1957–61 data
38	225,000	167,000 (15)
41	310,000	240,000 (34)
44	175,000	420,000 (63)
47	330,000	554,000 (67)
50	200,000	673,000 (20)
53	660,000	847,000 (17)
56	...	1,207,000 (5)
59	725,000	1,380,000 (5)
62	750,000	1,748,000 (1)
65	...	2,158,000 (1)
68	730,000	...
71	1,300,000	...

FECUNDITY RELATED TO WEIGHT

Gutted weights (less weights of gills) are available only for the 167 specimens collected in 1957, 1958 and 1960. When the estimated fecundities are plotted against these weights individually, it is seen that for any one length of fish the fecundity varies widely as mentioned before for the fecundity–length relationships. However, a linear trend is indicated and this is shown in Fig. 3 by the broken line.

Since fecundity has been shown to increase at a rate close to the fifth power of the length instead of length cubed, it was considered necessary to examine the relationship between length and gutted weight for the present data (Fig. 4). The log–log regression line fitted to the individual observations gives the relationship

$$W = 0.0000090\ L^{2.961}$$

which confirms the generally accepted fact that for haddock, as for most species of fish, weight is approximately proportional to the cube of the length. This being so, it would seem, therefore, that the relationship between log fecundity and log weight, when treated by the usual method of least squares, should produce an equation of the form $F = kW^n$, where n is of the order of about 1.7 ($n = 5.11$ for the log fecundity–log length relationship, and $n = 2.96$ for the log weight–log length equation; hence $n = 5.11/2.96 = 1.7$ for the log fecundity–log weight relationship). This is confirmed by the log fecundity–log weight regression line (Fig. 3), whose coefficient is also given in Table VI together with those for the data of the individual years and the corresponding coefficients of correlation.

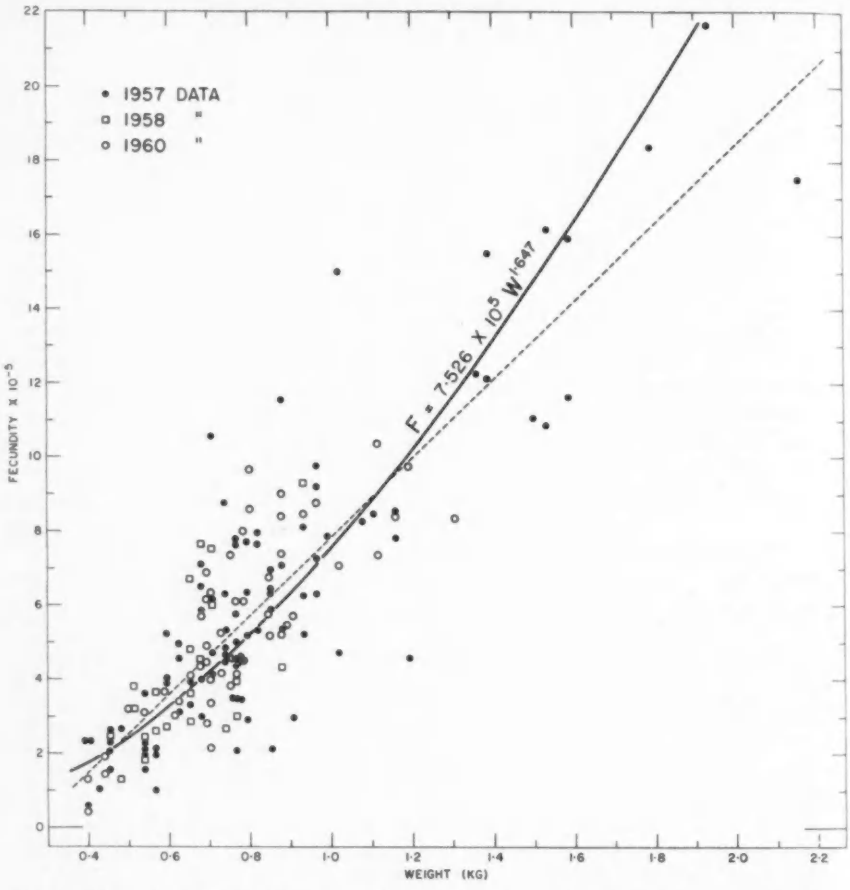

FIG. 3. Fecundity estimates for Grand Bank haddock by gutted weight and year of capture together with the fitted regression line (the broken line represents the linear relationship).

An analysis of covariance of these data does not indicate any significance between the slopes or the intercepts, but no weight data for 1959 are available here. The coefficients of correlation are slightly higher than those obtained from the fecundity–length analysis.

FECUNDITY RELATED TO AGE AND LENGTH

The haddock stock of the Grand Bank spawns along the narrow edge of the continental shelf known as the Southwest Slope (Fig. 1). Prior to the time of settling to the bottom, the pelagic larvae may be carried northward over parts of the Grand Bank where temperature conditions are unfavourable or southward over the depths of the ocean. Consequently great variation in year-class survival

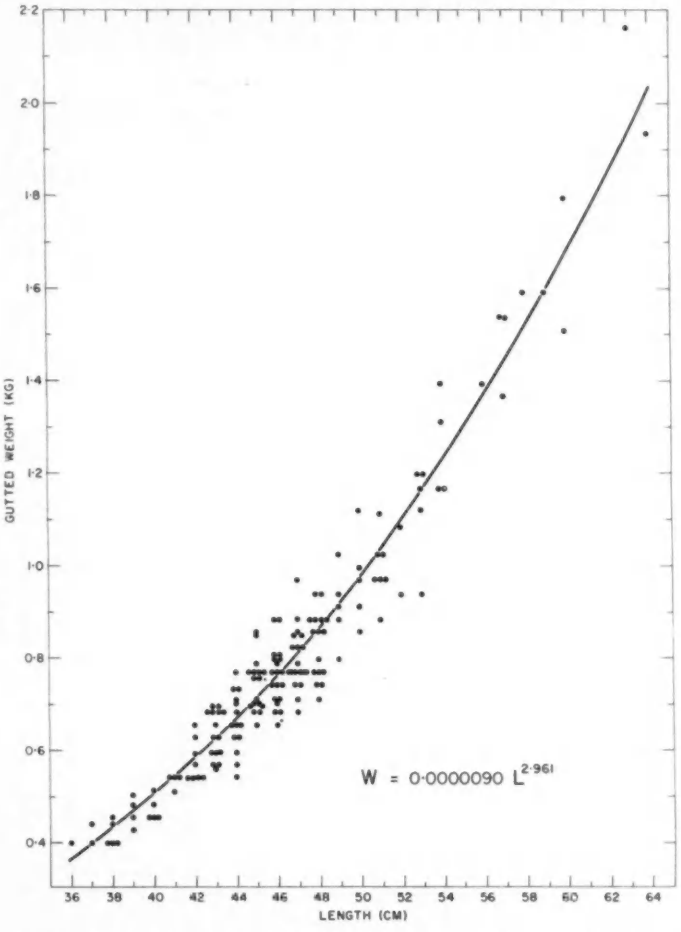

FIG. 4. The length–weight relationship of the female haddock specimens used for the fecundity estimations.

is inevitable and certainly does occur. This is borne out by the age distribution of the samples collected for fecundity estimates during the 1957–61 period (Table VII) and makes an analysis of fecundity data difficult in so far as making comparisons between years and ages are concerned.

The data are inadequate for certain ages, with observations either lacking in certain years when the data were collected or scanty in years when the samples were small. It will be noted that nearly a third of the total observations consist of 8-year-old fish collected in 1957. However, despite the inadequacy of the data with regard to age, there is a definite positive correlation between fecundity

TABLE VI. The relationships between log fecundity and log weight for the samples of 1957, 1958 and 1960. (N.S. = not significant at the 5% level.)

Year	No. of fish	Regression coefficient, n	Intercept log k	Correlation coefficient, r
1957	92	1.5838	5.8627	0.83
1958	23	1.6487	5.8909	0.66
1960	52	1.9376	5.9193	0.84
1957–60	167	1.6474	5.8767	0.83

Analysis of covariance for regression coefficients, F = 1.20, N.S.
Analysis of covariance for intercepts, F = 0.59, N.S.

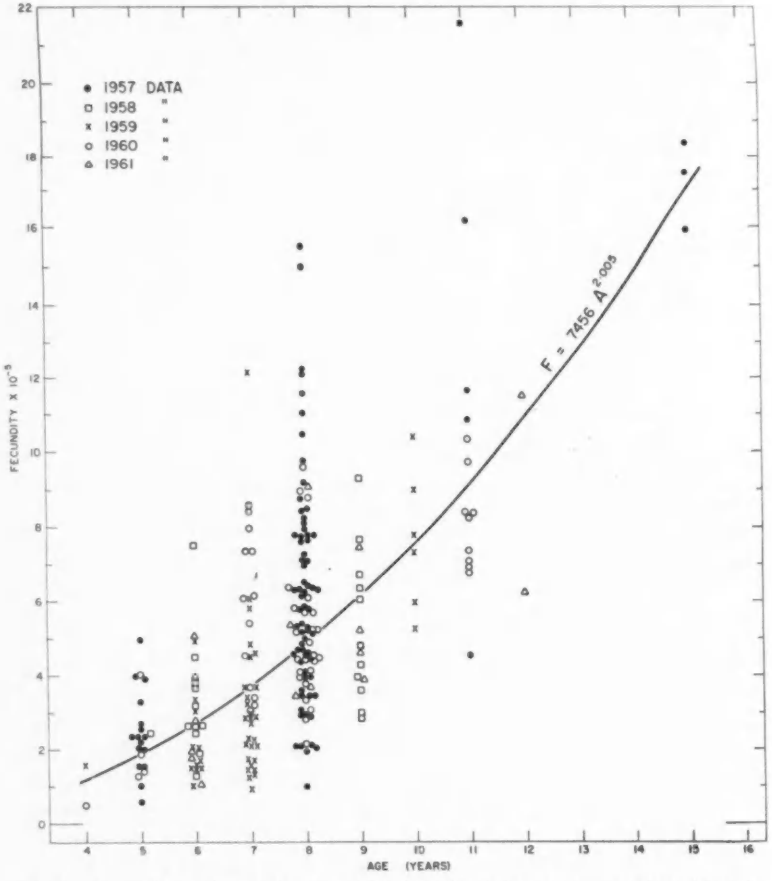

FIG. 5. Fecundity estimates for Grand Bank haddock by age, irrespective of length, and year of capture.

TABLE VII. Geometric mean fecundities by length groups for each age and year of capture.

Year of capture	Age (yr)	Geometric mean fecundities in thousands of ova by 2-cm length intervals															Geometric mean		Fecundity calculated from curve ('000)
		36–37	38–39	40–41	42–43	44–45	46–47	48–49	50–51	52–53	54–55	56–57	58–59	60–61	62–63	64–65	Length (cm)	Fecundity ('000)	
1957	5	...	152(5)	211(6)	318(4)	390(1)	...	...	...	...	...	...	...	...	...	...	40.5	220(16)	227
	8	...	...	...	298(6)	418(9)	496(21)	521(16)	814(8)	828(3)	1100(2)	1216(2)	...	1102(1)	...	...	47.7	550(68)	527
	11	...	...	...	...	...	...	...	...	455(1)	...	1324(2)	1160(1)	...	...	2158(1)	57.7	1148(5)	1380
	15	...	...	...	...	...	...	...	...	...	...	...	1588(1)	1834(1)	1748(1)	...	60.6	1720(3)	1780
1958	5	...	...	246(1)	...	...	...	...	...	...	...	...	...	...	...	...	41.0	246(1)	243
	6	...	176(2)	349(2)	265(4)	752(1)	345(2)	...	...	...	...	...	...	...	...	...	42.3	298(11)	283
	9	...	...	...	764(1)	488(3)	407(3)	298(1)	520(2)	931(1)	...	...	...	...	...	...	46.8	496(11)	480
1959	4	...	...	154(1)	...	...	...	...	...	...	...	...	...	...	...	...	40.0	154(1)	213
	6	...	127(2)	184(3)	197(3)	492(1)	223(2)	...	...	...	...	...	...	...	...	...	42.1	198(11)	277
	7	...	...	175(5)	188(9)	261(5)	379(5)	527(2)	...	578(1)	...	...	1216(1)	...	...	...	44.3	267(28)	360
	10	...	...	...	...	...	728(1)	778(1)	...	688(3)	900(1)	...	...	...	...	...	50.9	742(6)	735
1960	4	...	48(1)	...	...	...	...	...	...	...	...	...	...	...	...	...	37.0	48(1)	144
	5	137(2)	191(1)	...	402(1)	...	...	...	...	...	...	...	...	...	...	...	38.2	195(4)	170
	7	...	320(1)	...	326(3)	532(3)	658(5)	843(1)	...	...	...	...	...	...	...	...	44.4	514(13)	363
	8	...	...	...	385(4)	431(13)	640(5)	686(2)	570(1)	...	...	...	...	...	...	...	45.2	481(25)	400
	11	...	...	...	...	689(1)	754(2)	705(1)	735(1)	1002(2)	834(2)	...	...	...	...	...	50.1	805(9)	673
1961	6	...	138(2)	...	273(1)	278(2)	504(1)	...	...	...	...	...	...	...	...	...	42.3	242(6)	283
	8	...	...	...	578(2)	347(1)	...	...	536(1)	...	...	...	...	...	...	...	44.7	499(4)	377
	9	...	...	...	...	743(1)	465(1)	520(1)	388(1)	...	...	...	...	...	...	...	47.2	514(4)	500
	12	...	...	...	...	...	...	...	...	...	846(2)	...	...	...	...	...	54.0	846(2)	990
1957–61	4	...	48(1)	154(1)	...	...	...	...	...	...	...	...	...	...	...	...	38.5	86(2)	177
	5	137(2)	158(6)	216(7)	333(5)	390(1)	...	...	...	...	...	...	...	...	...	...	40.0	216(21)	213
	6	...	146(6)	237(5)	238(8)	411(4)	312(5)	...	...	...	...	...	...	...	...	...	42.2	243(28)	280
	7	...	320(1)	175(5)	216(12)	341(8)	499(10)	616(3)	...	578(1)	...	...	1216(1)	...	...	...	44.4	328(41)	363
	8	...	...	...	362(12)	422(23)	545(26)	537(18)	754(10)	828(3)	1100(2)	1216(2)	...	1102(1)	...	...	46.9	529(97)	483
	9	...	...	...	764(1)	542(4)	421(4)	394(2)	472(3)	931(1)	...	...	...	...	...	...	46.9	501(15)	483
	10	...	...	...	...	...	728(1)	778(1)	...	688(3)	900(1)	...	...	...	...	...	50.9	742(6)	733
	11	...	...	...	...	689(1)	754(2)	705(1)	735(1)	770(3)	834(2)	1324(2)	1160(1)	...	...	2158(1)	52.7	914(14)	877
	12	...	...	...	...	...	...	...	...	...	846(2)	...	...	...	...	...	54.0	846(2)	990
	15	...	...	...	...	...	...	...	...	...	...	...	1588(1)	1834(1)	1748(1)	...	60.6	1720(3)	1780

and age (Fig. 5), although the variation in fecundity for the same age is seen to be even greater (correlation coefficient r is 0.66) than that observed between fish of the same length or weight. The weighted log–log regression line fitted to the fecundity–age data indicates that, in general, fecundity increases at a rate proportional to the square of the age.

Since fecundity increases with both length and age, it is necessary to examine the data with these two factors separated, and this is shown in Fig. 6, where fecundity is plotted against length for ages 5–8. The log–log regression lines are also shown, the regression coefficients of which are 6.39, 4.25, 5.69 and 4.23, respectively. The curves for ages 6 and 7 (solid lines) are heavily weighted by the low fecundity estimates of the 1959 data, while those for ages 5 and 8 are entirely unaffected. When the 1959 observations are omitted from the regression analysis for ages 6 and 7, the regression coefficients for these ages become 4.93 and 4.90, respectively.

Since age-4 spawners are not common among female haddock of the Grand Bank and none spawn earlier than this age, most of the mature 5-year-old females are first-time spawners. Among 8-year-old females, nearly all are mature and many are spawning for the third and fourth times. It is possible, therefore, that the decrease observed in the regression coefficients of the log fecundity–log length curves by age might be related to the relative decrease in the proportion of first-time spawners with age. Raitt (1933) found for North Sea haddock that 2-year-olds which are all first-time spawners gave a regression coefficient of 4.88, whereas the range for older ages fell between 3.21 and 3.29. However, one fact is evident here as noted previously that even within any one age the variation in individual fecundity at length of fish is still great.

It was noted above that when the 1959 observations are omitted from the regression analysis for 6-year-olds the regression coefficient increases from 4.25 to 4.93, whereas for 7-year-olds the regression coefficient decreases from 5.69 to 4.90. Actually the regression coefficients for ages 6 and 7 of the 1959 data only are 3.42 based on 11 observations and 5.80 based on 28 observations, respectively. The 1959 observations were taken at sea during the course of a trawl survey over the southern half of the Grand Bank from depths ranging between 47 and 148 fathoms, whereas the samples in the other years were taken from depths between 42 and 105 fathoms. Examination of the catch records reveals that all but one of the 6-year-olds were taken in less than 105 fathoms, whereas nearly a third of the 7-year-olds and most of the 10-year-olds were caught in depths between 117 and 148 fathoms. The latter were in nearly all instances more fecund than specimens taken from shallower depths. When these deep-water specimens are removed from the regression analysis for 7-year-olds of 1959, the regression coefficient becomes 5.18 which is now not very different from the value of 4.90 observed for the 7-year-olds of 1960.

In Table VII are shown the geometric mean fecundity estimates by length and age for the samples of 1957–61 separately and combined. The last 3 columns of the table give the geometric mean lengths of fish and fecundity estimates by age together with the corresponding fecundity values as calculated from the

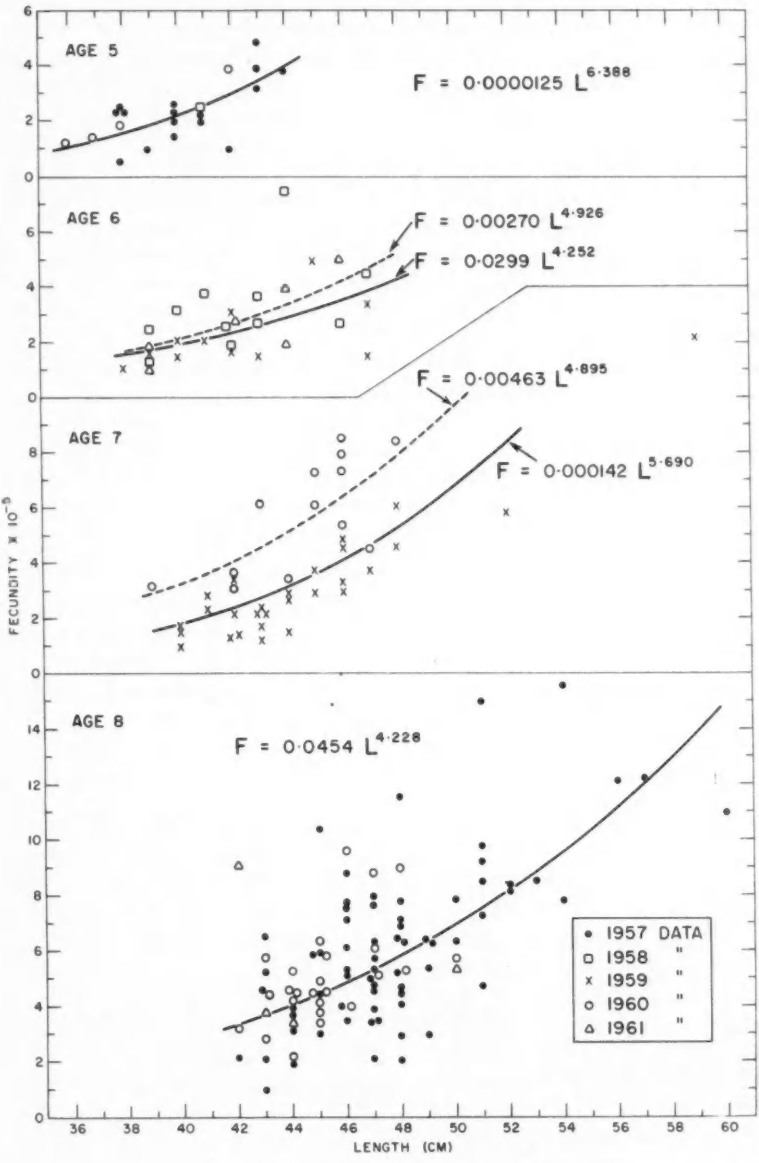

FIG. 6. Fecundity estimates for Grand Bank haddock by length and year of capture for ages 5–8 separately (the broken curves represent the relationships when the 1959 fecundity estimates are omitted).

curve of Fig. 2. The similarity of the observed and calculated fecundity values for 1957 and also for 1958 must be noted. For 1959 the fecundity estimates as observed for ages 6 and 7 are substantially below the calculated values, whereas the observed and calculated values for age 10 are similar. As noted previously most of these age 10 fish were caught in deep water over 100 fathoms, where they probably migrated at an earlier age and where they were not as liable to be affected by the violent changes in environmental conditions that may occur at shallower depths along the southwest slope of the Grand Bank. In 1960 the observed fecundity values for ages 5–11 are considerably greater than those calculated from the curve. In 1961, except for age 8, the observed and calculated values are reasonably similar considering the small numbers of observations involved. The significance of the variation in fecundity observed in 1959 and 1960 is discussed in a later section.

Because fish of certain ages were not well represented in the annual samples, the fecundity–length relationships for certain years are influenced more than others by the apparent annual variation in fecundity. Consequently it is not feasible to use the pooled data (Table VII) in considering whether or not fecundity varies with age for fish of the same length. However, examination of the data by individual years indicates that for haddock of the same length interval the younger fish are in general just as fecund as the older ones.

Fecundity Related to Number of Spawnings

In an effort to account for the great variation among fish of the same age, an attempt is made to relate the fecundity of haddock with the number of times that the fish had spawned. This was not possible from the present data directly, since the determination of spawning zones in bony structures such as scales and otoliths is not reliable at present for this species. However, preliminary assessment of unpublished data on maturity of Grand Bank female haddock indicates that about 2% of age 4, 28% of age 5, 70% of age 6, 90% of age 7 and 98% of age 8 are mature. Since no females of age 3 have been known to mature, all the mature 4-year-olds are spawning for the first time, this being 2% of all age-4 females. Consequently 2% of all age-5 females are spawning for the second time, leaving 26% as spawning for the first time. Of all age-6 females, we may assume that 2% are spawning for the third time and 26% for the second time, leaving 42% as spawning for the first time. By carrying this method of determining the frequency of spawning through to age 8, the relative proportions of fish spawning for the first, second, third, fourth and fifth times at each of the ages 4–8 may be calculated from the frequency distribution of ages in the present data (Table VIII). When the spawning frequency distributions by age up to 8 years are compared with the corresponding frequency distributions based on maturity data by means of chi-square tests, the agreement is remarkable. This analysis has not been applied to the data for ages greater than 8 because of relatively few observations. If the 1959 fecundity estimates for age 7 were adjusted upward to bring them more in line with those for other years, the chi-square value for this age is considerably less than that given in Table VIII and the P-value somewhat higher.

TABLE VIII. Comparison of the frequency distribution of spawners based on maturity data with the assumed frequency distribution based on fecundity estimates.

	Frequency distribution based on maturity data		Frequency distribution based on fecundity estimates			
Age	No. of spawnings	Expected frequency	Range of fecundity	Observed frequency	χ^2	P-Value
			('000)			
4	1st	2	48– 158	2	...	...
5	1st	19	58– 249	14	...	P = 0.07
	2nd	2	250– 496	7		
6	1st	17	102– 249	14	1.347	.3 > P > .2
	2nd	10	250– 449	11	df = 1	
	3rd	1	450– 752	3		
7	1st	9	95– 249	14	5.664	.1 > P > .05
	2nd	19	250– 449	12	df = 2	
	3rd	12	450– 749	11		
	4th	1	750–1216	4		
8	1st	8	101– 249	7	2.436	.5 > P > .3
	2nd	19	250– 449	25	df = 3	
	3rd	42	450– 749	40		
	4th	26	750–1250	23		
	5th	2	1250	2		

Raitt (1933) found for North Sea female haddock that about 11% at age 2, 75% at age 3, 96% at age 4 and 99% at age 5 are mature. He points out that within each age-class the percentage of mature fish increases with length and that the average length of immatures of an age-class is always less than that of matures. This fact is confirmed for Grand Bank haddock from unpublished maturity data. It would seem, therefore, that the incidence of first maturity is related to the rate of growth within an age-group. Since the larger fish of an age-group are more fecund than the smaller ones (Fig. 6), it is reasonable to assume that the fecundity of an individual fish is directly related to the number of times that it has spawned. In view of the remarkable agreement found between the spawning frequency distributions based on maturity data and on fecundity estimates, it is apparent that first-time spawners, regardless of age, generally produce up to 250 thousand ova, second-time spawners between 250 and 450 thousand ova, third-time spawners between 450 and 750 thousand ova, fourth-time spawners between 750 thousand and $1\frac{1}{4}$ million ova, and fish spawning for the fifth time or more produce more than $1\frac{1}{4}$ million eggs.

DISCUSSION

In Grand Bank haddock fecundity was found to vary at a rate proportional to about the fifth power of the length. This value of the exponent is considerably higher than those reported by other authors for this and other species. Mitchell (1913), from 19 fecundity estimates for North Sea haddock, observed that fecundity increased according to some power of the length, and she assumed that egg production is proportional to length cubed. Simpson (1951) for North Sea plaice (*Pleuronectes platessa*) expressed the relationship between fecundity and length by the "cube law", $F = kL^3$. He also examined the plaice data of several earlier investigators and concluded that in general there is a direct relationship between fecundity and the cube of the length. Raitt (1933) for North Sea haddock expressed the relationship between fecundity and length by an equation of the form, $F = kL^n$, and found that when all ages are considered together the value of the exponent was 3.84. Other authors, particularly Bagenal (1957a) for long rough dab (*Hippoglossoides platessoides*) of the North Sea, Nagasaki (1958) for Pacific herring (*Clupea pallasi*) and Thomson (1962) for Pacific cod (*Gadus macrocephalus*), have used this relationship and their values of n generally ranged between 3 and 4. However, for herring (*Clupea harengus*) of the northeast Atlantic, values ranging between 3.465 and 4.5 have been reported: Hickling (1940) obtained a value of 3.465 for southern North Sea herring, while Farron (1938) observed 4.5 for Irish Sea herring. This variation is attributed to the fact that Hickling's specimens were winter spawners and Farron's were spring and autumn spawners. Simpson (1951) found that, in North Sea plaice of the same length, the faster-growing fish from the Flamborough area had a higher fecundity than the slower-growing fish from the Southern Bight, but the fecundity of Baltic plaice was found to be so much higher than that of North Sea plaice that factors other than age and food must be involved. Perhaps the difference in the egg production patterns of Grand Bank and North Sea haddock (Fig. 7) may in some way be related to the delayed maturity of the Grand Bank population, but it is more likely that the difference is due to the peculiar characteristics of the 2 separate races.

When fecundity is related to age, irrespective of length, for Grand Bank haddock, it is found that there is a definite positive correlation between these 2 parameters, although the variation in fecundity at any one age is even greater than that observed between fish of the same length or weight. Also, fecundity increases at a rate proportional to the square of the age. Bagenal (1957a) for long rough dab found that the relationship between fecundity and age was approximately linear, and MacGregor (1957) used the linear regression analysis to compare Pacific sardine (*Sardinops caerulea*) samples. Hickling (1940) found for North Sea herring that the log fecundity–log age regression coefficient was less than 1 (actually 0.66). These authors all point out that the relationship between fecundity and age is not as good as that between fecundity and length or weight. Lehman (1953) also used the linear relationship between fecundity and age for Hudson River shad data (*Alosa sapidissima*), but found that the correlation between fecundity and age was better ($r = 0.98$) that than for fe-

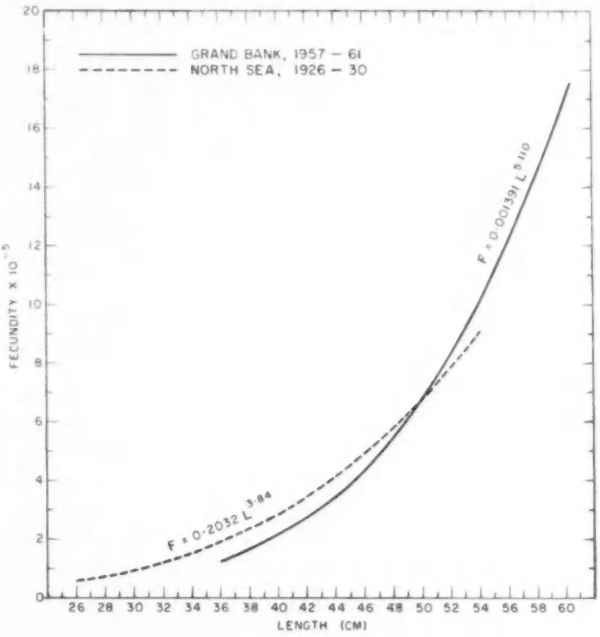

FIG. 7. The fecundity–length regression line for Grand Bank haddock and Raitt's (1933) curve for North Sea haddock.

cundity and length or weight; this, however, might be a peculiarity of the species. In any case, no explanation can be offered at present for the fact that the regression coefficients obtained from the fecundity–length, fecundity–weight and fecundity–age relationships for Grand Bank haddock are considerably higher than those previously reported for this and other species of fish in other areas.

Simpson (1951) found for North Sea plaice that the older fish were not more fecund than younger ones of the same size. The present fecundity observations appear to confirm this view, although Raitt (1933) reported for North Sea haddock that fecundity, in fish of the same size, was greater for older fish.

It has been shown that considerable variation in fecundity of Grand Bank haddock may occur from year to year. In particular, the 1959 fecundity estimates for fish of the same size and age were substantially lower than the averages for the 5 years combined (1957–61), while in 1960 the fish appeared to be generally more fecund. Such variation in annual egg production has not previously received much attention. The most important work in this regard is that of Bagenal (1957b) on long rough dabs for the years 1954–56. He points out that the fecundity in 1955 was significantly lower than that in 1954 and 1956, even after allowance was made for length differences. Similar significant differences were evident for fish condition. He does not offer any explanation for this,

except to point out that the differences were not due to differences in the age structure of the population.

In discussing the variation in fecundity of individual plaice, Simpson (1951) observes that there are at least 2 critical periods in which the number of eggs to be laid may be influenced: one is the period when the germinal epithelium is being laid down during the first year of life, and the other is either the time when the new primary oocytes are being formed each year or when the eggs to be laid in the next spawning season are separated from the mass of resting oocytes. Since the first possibility might fix the fecundity potential of the fish for life, it must be discounted here. Simpson's second critical period should really be called the second and third critical periods, for a considerable period of time might elapse between the formation of the primary oocytes and the separation from the mass of resting oocytes of the batch of ova for spawning in a subsequent spawning season.

According to Simpson (1951), it has been pointed out by Franz (1910) and Reibisch (1899) that once maturity is first reached 2 or 3 years elapse between the formation of oocytes and the final liberation of the resulting eggs, the eggs to be spawned in any winter being separated from the resting oocytes during the summer immediately preceding spawning. Raitt (1933) has thoroughly reviewed the literature with regard to intra-ovarian egg groups. From this and from his own observations on North Sea haddock he concludes that in ripening ovaries 2 separate groups of ova are present (opaque-yolked and transparent-yolkless eggs), the first group to be laid in the approaching spawning season and the second to be laid in the following or possibly succeeding years.

Assuming that the period of intra-ovarian development is 2 years and that the critical period is the time of formation of the oocytes, it is possible that the low fecundity of haddock in 1959 and the high fecundity in 1960 might be the result of environmental conditions existing during the spring of 1957 and 1958, respectively. Examination of air temperature records published monthly by the Meteorological Division of the Canadian Department of Transport (Anon., 1952–61) reveals that in Newfoundland the winters of 1957 and 1959 were unusually cold and that the winter of 1958 was warmer than the more normal conditions of 1953 to 1956 (Fig. 8). The mean air temperatures at St. John's Airport for the period January to March of the years 1955–59 were as follows:

Year	°*F*	°*C*
1955	27.6	−3.0
1956	26.8	−2.9
1957	21.6	−5.8
1958	30.0	−1.1
1959	21.2	−6.0
1952–61	26.0	−3.3

Templeman (1958, 1959, 1960) from hydrographic evidence points out that during the summers of 1957 and 1959 bottom temperatures on the southern Grand Bank were unusually low, whereas in 1958 they were generally above normal.

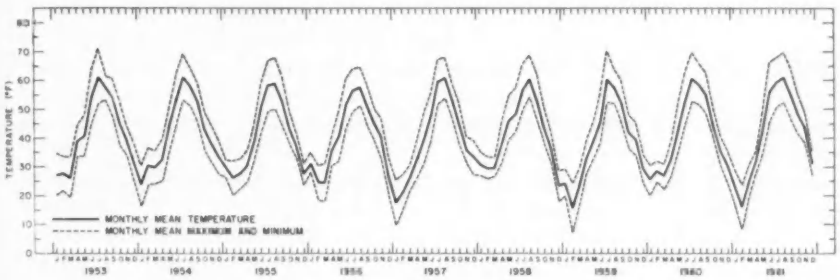

FIG. 8. Mean monthly air temperatures at St. John's Airport, 1953–61, with their corresponding mean maximum and mean minimum air temperatures.

During the winter months haddock are generally concentrated in deep water, usually below 50 fathoms, along the southwest slope of the Grand Bank. At this time the shallower parts of the bank are completely covered with cold water of less than 1° C and often there is much water below 0° C. In a year like 1957, when an unusually large volume of cold water flowed southward along the east coast of Newfoundland and covered the Grand Bank for a longer-than-normal period, the haddock were forced deeper and became very heavily concentrated along the narrow southwest slope. The resulting overcrowded conditions, in which lack of food supposedly restricts growth, as argued by Lack (1954), probably had the effect of reducing the fecundity of haddock 2 years later in 1959. In 1958, on the other hand, the higher-than-normal temperature conditions that existed throughout most of the area caused the haddock concentrations to be dispersed from their winter quarters a month or more earlier than usual, thus favouring good growth in the spring and summer and consequently greater egg production 2 years later in 1960. Hydrographically, the years 1955 and 1956 were more or less typical of the average conditions in recent years. Conditions in 1959 were somewhat similar to those of 1957, but the small number of fecundity observations in 1961 are not sufficient to conclude whether or not the fecundity was lower than average in that year.

If, as Franz (1910) and Reibisch (1899) suggest, the eggs to be spawned in an approaching spawning season are separated from the resting oocytes during the preceding summer, and if we consider this period as a critical one, then the environmental conditions existing in 1958 and 1959 may have been responsible for the low fecundity of haddock in 1959 and the higher-than-average estimates for 1960. Assuming that, for any particular ovary, the surface area of the lamellae on which egg growth can continue is limited (by the size of the ovary), it follows that the number of eggs for spawning in the following year is related not only to the size of the ovary but also to the size of the eggs at the time when the limit of coverage of the basic surface area is reached. If this is so, then fecundity might be related to the function of growth which these eggs undergo during the short period in the summer when they are being separated from the resting oocytes. Thus, in a year when growth conditions are very favourable, it is

possible that fewer large oocytes will occupy the available surface area of the ovarian lamellae and consequently result in lower fecundity at spawning time of the following year. If conditions are unfavourable, thus restricting egg growth, a larger number of small oocytes may now occupy the available surface area of the ovary with the end result of higher fecundity in the next spawning season.

Perhaps the number of eggs produced by an individual fish in any one spawning season is the result of environmental conditions during the several months immediately preceding spawning. Vladykov (1956) for wild speckled trout (*Salvelinus fontinalis*) in Quebec lakes says that an abundant food supply for adults during several months preceding spawning resulted in higher fecundity at spawning time. Scott (1962) carried out experimental diet restriction on rainbow trout (*Salmo gairdneri*) and found that starvation during the year preceding spawning influenced the number of eggs by increasing the rate of atresia. Although there is no evidence at present to indicate that follicular atresia plays a very significant role in the fecundity of marine fishes which produce large numbers of small pelagic eggs, it is possible that severe food restriction during a period of several months preceding spawning may induce some reabsorption of eggs. To this extent, then, overcrowding during the winter and spring of 1959, caused by the abnormally low-temperature conditions, may have resulted in low fecundity at spawning time of that year. Much of the above discussion is speculative, since the effect of such factors as temperature on the processes of growth and reproduction in fish is not fully understood.

Nowhere in the literature surveyed by the author has any attention been given the possible relationship between the fecundity of individual fish and the number of times that the fish has spawned. While it is not possible from the present data alone to obtain a direct relationship between frequency of spawning and egg production, the comparison of other maturity data and the present fecundity data does give some indication of a possible connection. The suggestion is offered here so that it might form the basis for future work in this regard on species for which the spawning zones can be reliably distinguished in otoliths or other bony structures.

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Minke Whales, *Balaenoptera acutorostrata* Lacépède, of the Western North Atlantic[1]

By D. E. Sergeant

Fisheries Research Board of Canada
Arctic Unit, Montreal, P.Q.

ABSTRACT

Minke whales *Balaenoptera acutorostrata* support a shore-based fishery in eastern Newfoundland. The appearance of minke whales here parallels the spawning concentration of capelin (*Mallotus villosus*) and lasts from late May to late July, the whales eating chiefly capelin with some cod and herring and other organisms. Summer distribution extends north to Ungava Bay. A return migration is not noted in Trinity Bay before catching ends in late October but reports from the Labrador coast indicate that many whales pass through just before freeze-up in November or December. The catch in Newfoundland consists mainly of large mature animals, and there is some evidence that many calves may remain in summer in more southerly waters. Body form, colouration and life cycle show no differences from minke whales of European seas. Ear plugs were rarely found to show readable growth layers in minke whales.

INTRODUCTION

In the past, the study of the minke whale, *Balaenoptera acutorostrata* Lacépède (also known as the lesser rorqual or little piked whale) in the western North Atlantic has been limited, by the absence of a fishery for this species, to reports on sightings, strandings, or occasionally captured animals. A fishery for the smaller kinds of whales which began on the east coast of Newfoundland in 1947 has provided material for a more detailed study. This fishery was mentioned previously in the biological literature by Scattergood (1949), who compiled an extensive literature on the species. Latterly minke whales have been well studied in the northern hemisphere; we shall not discuss work on southern hemisphere minke whales. Jonsgaard (1951, 1962) made extensive studies on minke whales taken by the Norwegian small-whale fishery between the North and Barents Seas, and Stephenson (1951) reported on minke whales taken by the same fishery around Great Britain, while both these writers compiled data on foetal lengths taken from their own observations and from the literature. Omura and Sakiura (1956) published a study of minke whales taken around Japan, using extensive statistical data supplemented by first hand observations. They also compiled data on animals stranded or captured on the west coast of North America, and made racial comparisons between minke whales from the North Atlantic and North Pacific. A previous comparison of this kind, based on smaller data, had been made by Cowan (1939).

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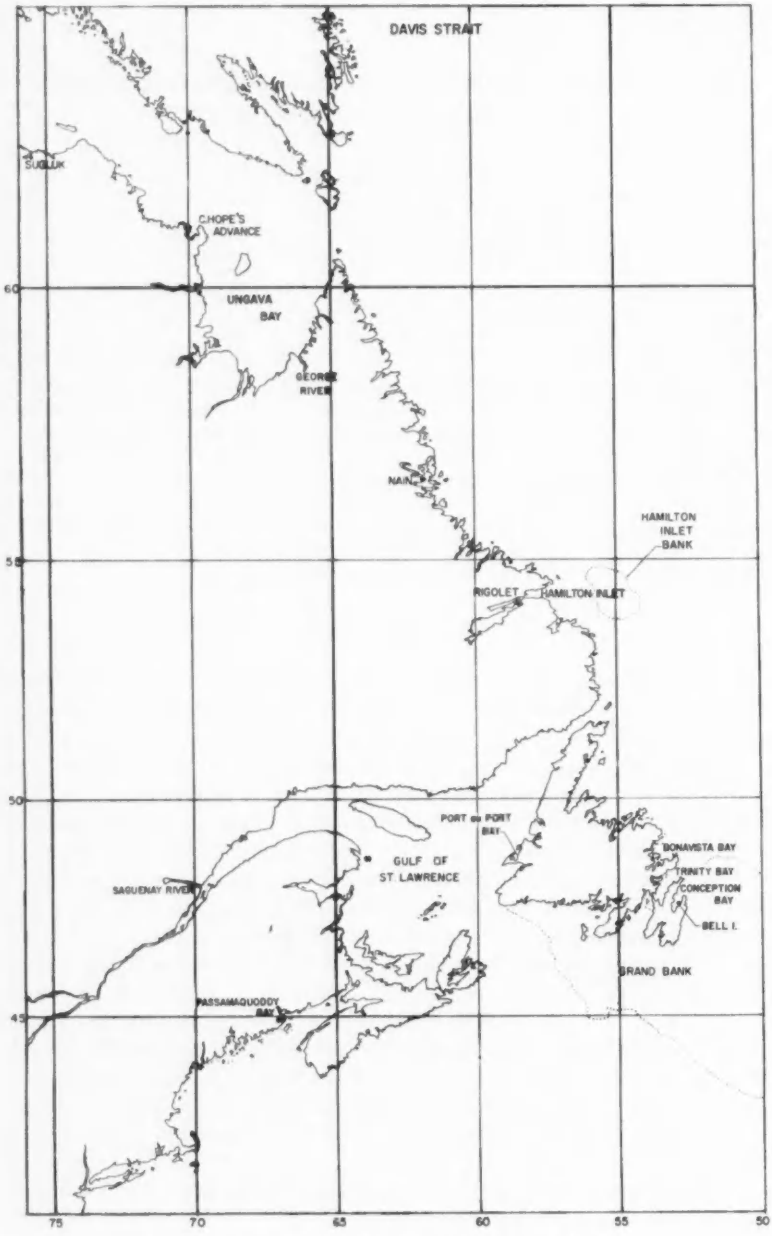

FIG. 1. Map showing place names mentioned in text.

THE FISHERY IN NEWFOUNDLAND

Minke whales have been taken annually since 1947 in Conception and Trinity Bays with a few in Bonavista Bay on the east coast of Newfoundland (Fig. 1). One to three Norwegian-type catching vessels fitted with 50-mm whale cannon have been used in different years. The whales are towed to a shore station for flensing, giving good opportunity for biological study. First-hand study of large numbers of whales has not been possible, however, because the range of a shore-based operation is limited and few whales are taken in any one year. The fat and meat from the catch of 10–60 whales per annum are added to the normally much larger quantities obtained from pilot whales (*Globicephala melaena* Traill), the meat being used principally as food for ranch mink (*Mustela vison*). Before the development in 1954 of intensive mink ranching in Newfoundland, a quantity of the better meat from minke whales was sold for human food, but a market was developed only in Newfoundland. The main incentive to pursuing the minke whales is that the whaling season is thereby extended 1 or 2 months before the arrival of the pilot whales, which are present in the bays from July to October (Sergeant and Fisher, 1957).

Figure 2 shows the catch by months for a number of years. Catching in some years has started in May, but since whales are then scarce, the weather is

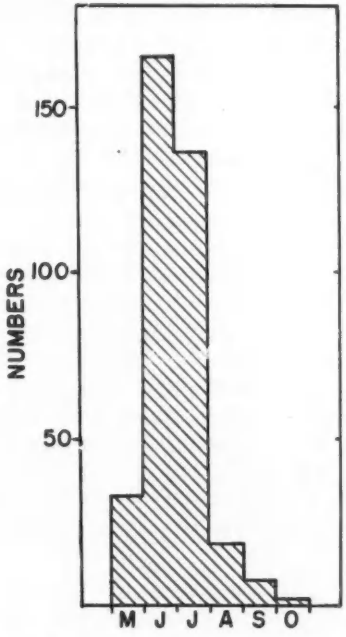

FIG. 2. Catches of minke whales in eastern Newfoundland, by months, 1948 and 1951–61.

cold and ice is often present in the bays, the boats are not normally commissioned until more intensive catching becomes possible in June. As soon as the pilot whales arrive in their turn, the catchers attempt whenever possible to drive them. Nevertheless the herds of pilot whales are hard to find at times in late summer, and in some summers fail to arrive at all, so that considerable opportunities still exist to continue the hunt for minke whales. Thus the paucity of catches in August and September reflects a real scarcity of minke whales, which seem to leave Trinity Bay at the end of the season of abundance of capelin in late July or early August (see below). The writer made arerial surveys of cetaceans covering much of Conception and Trinity Bays on August 29, 1957 and September 27, 1956. On the August flight one minke whale was seen, close to Bell Island, Conception Bay, and on the September flight none.

BIOLOGY

Data on standard length, sex and stomach contents of the animals and length of foetus come from whaling statistics compiled by the whaling company for the Department of Fisheries of Canada in St. John's, Newfoundland. Those available to the writer cover the years 1948 and 1951 to 1961, and relate to some 360 animals. Lengths in 1958 are unreliable and have had to be discarded; in other ways there seems no reason to doubt the general level of accuracy of the statistics. My own studies during July and August of 1953 and 1954 were incidental to an intensive study of pilot whales and data of varying completeness were obtained from 26 minke whales. In 1957 a special study of minke whales was made during June and early July, and data obtained from 17 animals relating to lengths, body proportions, stomach contents, reproductive condition, and the use of baleen plates and ear plugs for age determination.

External Characters

The general form and colouration of the species are well known and are illustrated by the photographs in Fig. 3. Omura and Sakiura (1956) described and figured a wavy anterior margin to the white band of the flipper for minke whales from the North Pacific and noted that a straight border was shown in a photograph of the flipper of a minke whale from Florida figured by Moore and Palmer (1955). Drawings of three flippers and photographs of two more from minke whales caught in Newfoundland (one shown in Fig. 3) show a relatively straight border to the white region, but there is considerable variation in its exact form — sometimes broadly convex, sometimes a shallow sinusoid. Also the white region may start abruptly, or may be preceded by a broad "shadow" of light grey (Fig. 3).

The baleen in our animals was cream-white in colour, a small percentage of the plates in some animals having a dark grey outer edge about 4 cm in depth. The number of baleen plates was counted in two animals, a 24-ft (7.3-m) female having 293 and 287 free plates, a 25½-ft (7.8-m) female, 315 and 320. As might be expected, these fall closer to the mean of 304 free baleen plates found by

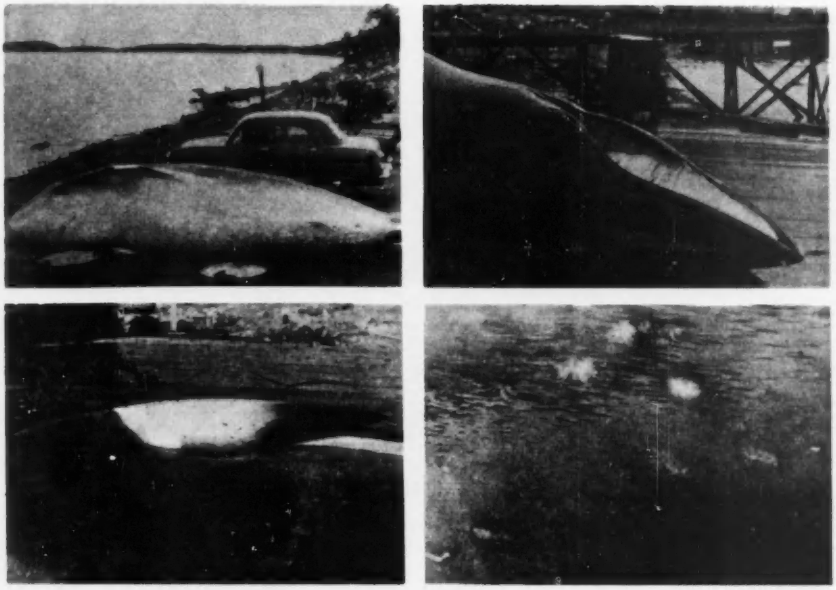

FIG. 3. Male minke whales at South Dildo whaling station, August 25, 1953 and August 1, 1959. Both animals 24 ft (7.3 m) in length. *Above, left:* ventral view. Note scars on abdomen possibly caused by lampreys. *Above, right:* dorsal view of head showing baleen. *Below, left:* dorsal view of right flipper. *Below, right:* scars on belly.

Jonsgaard (1951) for minke whales from the northeast Atlantic than the mean of 280 (never exceeding 300) found by Omura and Sakiura from the North Pacific. These authors associate the smaller number of plates for North Pacific minke whales with the shorter length of the mouth found by them from body-proportion measurements. They do not mention a grey border to the baleen plates in any of 26 animals examined by them. Cowan's (1939) fresh specimen from the coast of British Columbia had plates "pale horn colored shading to dirty white at the anterior end of the series". This 15-ft (4.6-m) animal was a juvenile without the full number of baleen plates, having only 230 of them.

Standard body measurements were made on 30 animals. The data are shown in Table I, and compared with corresponding measurements given by Jonsgaard for a larger series of minke whales taken in the Norwegian and Barents Seas. There appear to be no significant distinctions between minke whales from the two areas.

LENGTH FREQUENCIES

Length frequencies obtained from the statistics and relating to 143 males and 154 females are shown in Fig. 4. Although female minke whales grow to a somewhat larger size, as shown by both Jonsgaard (1951) and Omura and Sakiura

TABLE I. Measurements of body dimensions on minke whales.

1. Total length.
2. Lower jaw, projection beyond tip of snout.
3. Tip of snout to the anterior end of the blow-hole.
4. Tip of snout to centre of eye.
5. Tip of snout to tip of flipper.
6. Eye to ear (centres).
7. Notch of flukes to posterior emargination of dorsal fin.
8. Notch of flukes to anus.
9. Notch of flukes to umbilicus.
10. Notch of flukes to end of ventral grooves.
11. Notch of flukes to the nearest part of the anterior margin of the flukes.
12. Flukes, notch to tip.
13. Anus to reproductive aperture, centres.
14. Dorsal fin, vertical height.
15. Flipper, tip to axilla.
16. Flipper, greatest width.
17. Flipper, tip to head of humerus.
18. Head length, condyle to tip of snout.
19. Tail, depth at dorsal fin.

Norwegian Arctic

	Females			Males		
Specific measurement (see above)	Number measured	Range of total length (*cm*)	Mean length (*cm*)	Number measured	Range of total length (*cm*)	Mean length (*cm*)
1	75	480–914	735	24	488–828	658
Specific measurement (see above)	Number measured	Range of dimensions as percentages of total length	Mean percentages	Number measured	Range of dimensions as percentages of total length	Mean percentages
2	21	0.88– 2.41	1.56	13	1.15– 2.45	1.84
3	52	10.97–14.85	13.18	20	11.86–14.10	13.01
4	75	15.73–19.33	18.05	24	17.05–20.00	18.33
5	73	36.76–46.47	43.43	24	36.87–46.50	43.57
6	74	4.64– 6.19	5.50	24	4.91– 6.19	5.55
7	73	26.39–32.13	29.29	24	27.76–33.29	29.97
8	75	18.67–30.13	25.99	24	24.75–28.46	26.23
9	74	37.33–52.01	46.00	23	43.31–50.08	46.79
10	74	43.48–58.67	51.54	24	47.73–56.48	52.19
11	75	5.81– 7.49	6.77	24	6.46– 8.10	7.03
12	74	12.00–15.38	13.90	24	13.17–15.36	14.05
13	75	2.71– 4.08	3.41	24	6.00– 8.48	7.27
14	72	2.93– 4.44	3.60	24	3.33– 4.58	3.94
15	75	8.78–12.38	9.99	23	9.00–14.40	10.19
16	75	3.20– 3.94	3.65	24	3.40– 4.18	3.70
17	75	11.75–17.07	15.24	24	13.51–16.88	15.43
18	51	20.54–25.81	22.50	20	20.77–24.80	23.25
19	72	10.63–17.10	13.43	23	11.49–15.37	13.68

TABLE I. (Continued)

	Newfoundland					
	Females			Males		
Specific measurement	Number measured	Range of total length (*cm*)	Mean length (*cm*)	Number measured	Range of total length (*cm*)	Mean length (*cm*)
1	16	511–861	736	14	556–826	739
Specific measurement	Number measured	Range of dimensions as percentages of total length	Mean percentages	Number measured	Range of dimensions as percentages of total length	Mean percentages
2	4	1.1– 2.6	1.7	3	1.0– 2.1	1.4
3	9	10.8–14.7	13.3	7	11.8–15.5	13.3
4	12	17.3–19.4	18.5	9	16.8–19.6	18.2
5	10	29.4–46.6	40.6	7	38.4–45.3	42.5
6	4	5.8– 6.2	5.9	3	5.1– 5.7	5.4
7	6	27.8–30.6	29.2	4	27.7–34.5	29.9
8	7	23.7–27.2	25.1	6	24.5–26.0	25.0
9	6	45.4–47.7	46.5	1	47.3	–
10	8	49.6–55.1	52.0	3	51.4–54.7	53.0
11	9	6.5– 7.4	7.0	7	6.3– 7.5	6.9
12	7	13.4–14.5	14.0	3	13.5–13.9	13.7
13	9	2.4– 5.6	3.4	5	6.5– 8.6	7.5
14	9	3.7– 4.8	3.9	7	3.7– 4.5	4.1
15	15	9.1–13.0	10.5	13	8.7–10.9	10.3
16	11	3.5– 4.1	3.8	9	3.4– 4.4	3.9
17	7	13.0–16.8	15.4	3	15.4–16.4	15.9
18	3	22.5–24.9	24.0	3	22.3–25.6	23.8
19	–	–	–	–	–	–

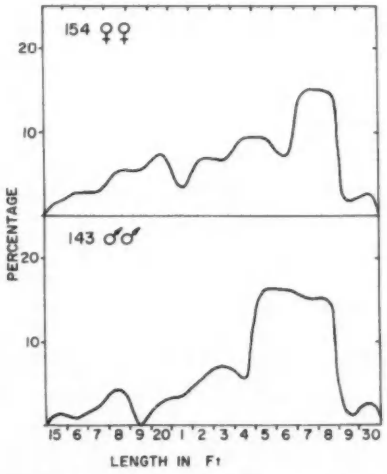

FIG. 4. Length frequencies of male and female minke whales from the statistics of catch in eastern Newfoundland.

(1956), the mean length is here somewhat greater for males (24.9 ft as compared with 24.4 ft for females), apparently because more immatures of females are present in the samples. Of 45 minke whales measured by the writer, 23 males ranged from 15 to 27 ft with a mean of 23.3 ft, and 22 females ranged from 15 to 29 ft with a mean of 24.9 ft.

Food

Capelin (*Mallotus villosus* O. F. Müller) is the dominant food organism in eastern Newfoundland. It was recorded in 85% of the stomachs in commercial statistics (Fig. 5). Capelin spawn from mid June to mid July on the beaches

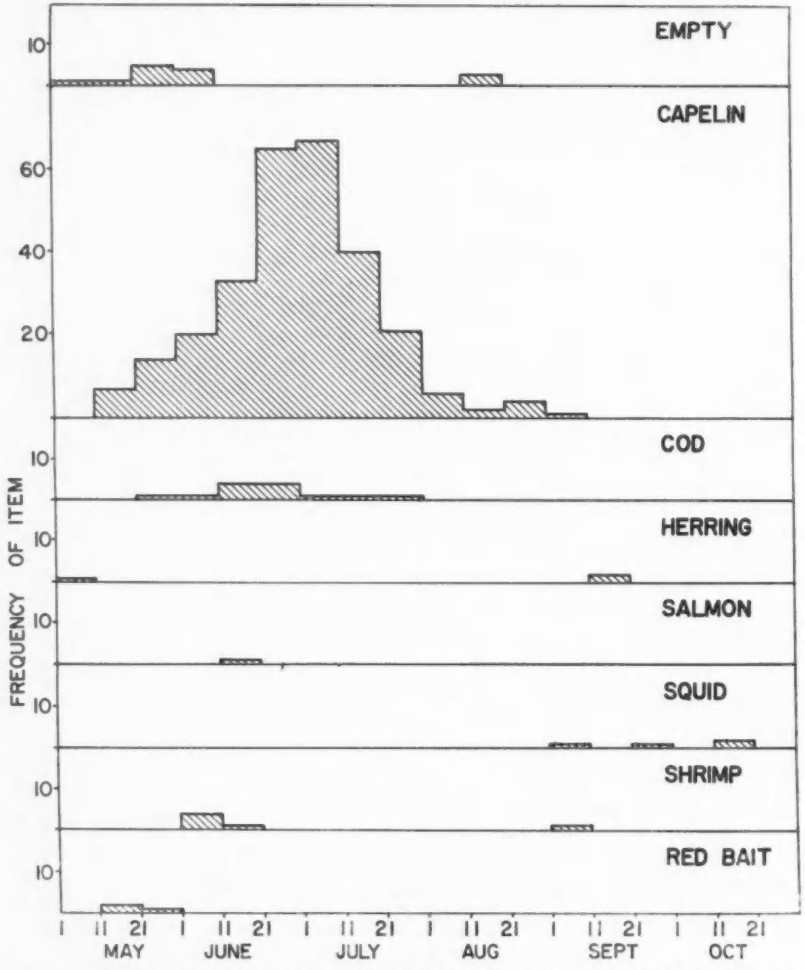

FIG. 5. Food of minke whales in eastern Newfoundland by 10-day periods, as reported in whaling statistics; 338 stomachs from 1948 and 1951–61.

of the bays of eastern Newfoundland, and for some time afterward in shallow water (Templeman, 1948), while they are probably present in shallow water for several weeks before spawning. The abundance of minke whales in these bays is therefore directly dependent on dense schools of capelin. Cod (*Gadus morhua* L.) is the next most frequent food species. Other foods recorded in the statistics include "red bait" (possibly copepods), "shrimp" (possibly euphausiids), squid (*Illex illecebrosus* Lesueur), salmon (*Salmo salar* L.) and herring (*Clupea harengus* L). Most of these foods are taken in small quantity before or after the capelin season, and empty stomachs were recorded only at these times (Fig. 5). In 32 stomachs examined by the writer in June and July the percentage frequency of occurrence of food organisms was capelin 83%, cod 9%, and herring 8%.

Reproductive Condition

Nineteen females were examined for reproductive condition between mid June and early August and details are given in Table II. Five immature females ranged in length from 16.8 ft (5.1 m) to 24.5 ft (7.5 m). These can be divided into two groups on the basis of ovary weight and follicle diameter (Table II and Fig. 6). The largest immature female, 24.5 ft (7.5 m) in length, showed a considerably enlarged mammary gland (22 × 8 cm) in cross-sectional diameter with open ducts; histologically the tissue showed secretory activity. One female

Table II. Reproductive condition of female minke whales.

No.	Length		Date	Condition	Ovary weights		Maximum follicular diameter	No. of corpora lutea and albicantia	Length of foetus
	ft	*in*			*g*	*g*	*mm*		*cm*
–	16	9	27/7/54	Immature	15	14	2.5	–	–
–	18	0	29/7/54	"	7	4	2	–	–
–	19	4	15/7/54	"	68	66	6	–	–
–	21	0	20/7/54	"	109	106	4	–	–
M 11	24	6	10/7/57	"	106	106	8	–	–
M 16	24	3	19/7/57	Ovulating	163	99	15	1 + 1	–
M 5	24	0	28/6/57	Pregnant	166.5	42	4	1 + 0	66
M 6	24	9	2/7/57	"	212	99	6	1 + 0	46
M 14	24	9	18/7/57	"	234	142	15	1 + 5	91
M 9	25	7	9/7/57	"	212	127	18	1 + 14	48
M 1	25	9	14/6/57	"	191	95.5	12	1 + 4	lost
M 13	26	±3	14/7/57	"	230.5	156	19	1 + 3	86
–	27	–	19/7/54	"	191	85	–	1 + 11	43
–	27	5	24/7/54	"	–	–	–	–	86
M 17	27	6	2/8/57	"	297	134	17	1 + 3	83
–	27	8	26/7/54	"	–	–	–	–	94
M 12	28	3	11/7/57	"	333	194.5	12	1 + 10	70
M 7	28	3	4/7/57	"	255	191	15	1 + 17	lost
M 4	29	±2	22/6/57	"	262	184	13	1 + 12	lost

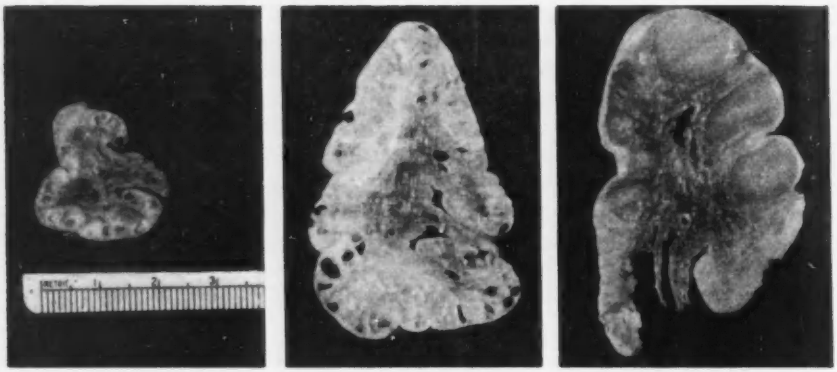

FIG. 6. Sections of ovaries of minke whales. Relative sizes and follicle diameters can be compared in (from left to right) a younger immature, older immature and mature, pregnant animal.

24.3 ft (7.4 m) in length taken in July had a full-sized corpus luteum and one old corpus albicans, and a uterus with swollen mucosa, though no foetus could be found. The remaining 12 females 24 ft (7.3 m) in length or greater were pregnant, with foetuses of from 43 cm to 94 cm in length. All ovaries examined from these animals contained enlarged follicles with maximal diameter ranging from 4 to 19 mm (Fig. 6). Lactation was not recorded in any pregnant animal and the mammary glands of 5 females examined histologically were in an advanced stage of involution. In the statistics, females were recorded pregnant at a length of 24 ft and upward.

Data on testis weights for 12 males are shown in Table III. All 12 males exceed the maximal length of immatures found by Jonsgaard (22.8 ft, 6.9 m) and have combined testis weights exceeding 225 g, the mean weight at sexual maturity found by him. Five testes were examined histologically, including the testis of the smallest male of this group, 22.9 ft (6.9 m) in length, and showed various stages of regression from active spermatogenesis.

TABLE III. Reproductive condition of male minke whales.

No.	Length		Date	Individual testis weights
	ft	*in*		*g*
M 15	22	10	19/7/57	120
–	23	6	24/7/54	300
–	24	–	18/7/53	460
–	24	–	24/7/54	550
–	24	5	24/7/54	ca. 500
–	24	8	26/7/54	500
–	25	–	26/7/54	365
M 2	25	2	20/6/57	175
M 8	26	1	8/7/57	300 500
M 3	26	±3	22/6/57	500
–	27	–	4/8/53	700 700
M 10	27	1	10/7/57	800 950

FOETAL LENGTHS

The Newfoundland statistics give lengths of 42 foetuses, usually to the nearest foot or half foot, for the period late May to early August with one in October. Of these, 10 were measured by the author to the nearest inch. Individual foetal lengths are plotted in Fig. 7. The measurements show a good grouping except for two aberrant lengths in late June. Whether these were

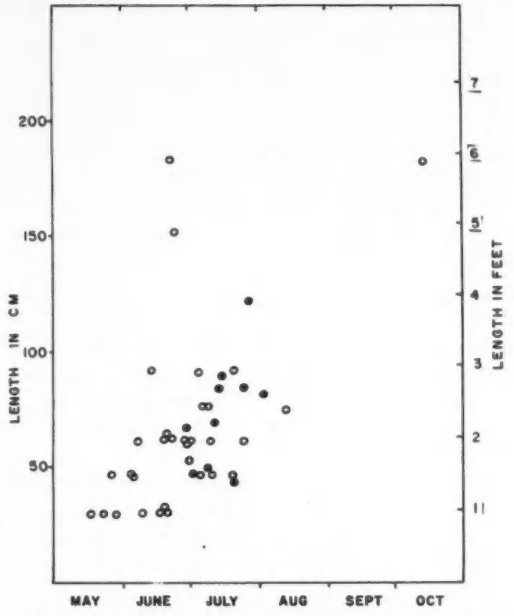

FIG. 7. Individual lengths of 42 minke whale foetuses from eastern Newfoundland, from statistics which include 10 measured by the author (solid circles).

errors, or foetuses from a distinct summer season of pairing, as found by Omura and Sakiura for about a quarter of North Pacific minke whales, cannot be settled. The only additional evidence for a summer pairing period in North Atlantic minke whales is the newly ovulated female in mid July mentioned above. No other investigators working in the North Atlantic have found foetuses of lengths suggestive of two annual pairing periods.

Figure 8 shows monthly means of foetal lengths of minke whales from the northeast Atlantic, from data of Jonsgaard (1951), Stephenson (1951) and Grieg (cited by Jonsgaard). A mean foetal growth curve has been fitted by eye to these data, making allowance for the fact that all material except Jonsgaard's was collected by whaling men and so likely tended to omit the smallest foetuses.

Means for 10-day periods of foetal lengths of minke whales from Newfoundland are also plotted in Fig. 8. Considering the approximate nature of most measurements, agreement with the European data is good.

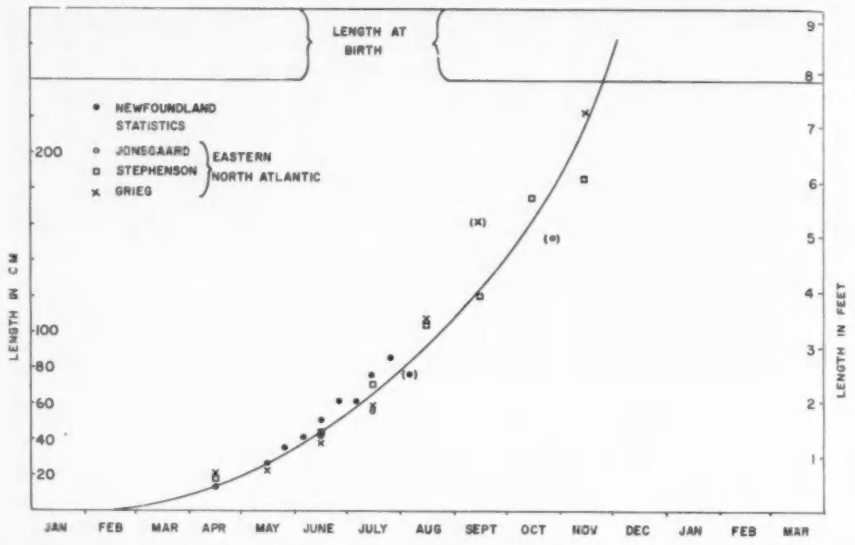

FIG. 8. Mean lengths of minke whale foetuses from Newfoundland for 10-day periods, and mean monthly foetal lengths recorded by observers from the northeastern Atlantic. A mean growth curve has been fitted by eye to the European data.

The estimates of length at birth in Fig. 8 come from statements of Jonsgaard and of Omura and Sakiura quoting other authors. The curve makes it appear likely that the mean period of pairings comes in February, the mean period of births in December, slightly earlier than estimated by Jonsgaard and more in line with the mean curve for winter-born calves given by Omura and Sakiura.

Thus our data fit Jonsgaard's conclusions that female North Atlantic minke whales mature sexually at about 24 ft and males at 22–23 ft; that the mating period extends over several months in late winter and that birth occurs in early winter; that there is an annual calf and lactation is short. From the absence of lactating females in Newfoundland waters in June we would also agree with Jonsgaard that the earliest weaning females probably migrate north earlier than those that have calved and weaned their calves later in the winter. There is as yet no firm evidence in the North Atlantic for a group of foetuses conceived in the summer months as found by Omura and Sakiura in the North Pacific, although further evidence should be sought on this point.

AGE DETERMINATION

Jonsgaard distinguished three length-groups of minke whales: animals about 16–18 ft in length, being calves in their first summer; those about 20 ft in length believed to be animals in their second year; and a group beginning at about 22 ft for males and 24 ft for females being animals in their third year and older. The two smaller groups of males were immature and could be separated into animals with smaller and larger testis weights, while males in the largest group

were nearly all sexually mature. Similarly the two groups of smaller females were sexually immature, the second having considerably greater ovary weights than the first, while most of the group of largest females were sexually mature. It seemed probable then that both males and females matured sexually at 2, with some at 3, years of age. However, the validity of Jonsgaard's length grouping is open to question in a species with so long a birth period. Omura and Sakiura (1956) distinguished two annual peaks in their length frequencies which they related to the two annual birth periods found by them in North Pacific minke whales. Using these peaks they also arrived at a tentative age of 2 years for age at maturity in both sexes.

In 1957 we collected ear plugs in order to try to determine age from this structure, following its use in fin whales by Laws and Purves (1956) and subsequently by many other authors. Extraction of the ear plug from the intact head was achieved by removing the fat over the region of the external ear opening and chipping away the maxillary and squamosal bones until the meatus was exposed. The ear plug could then be removed without damage.

Although it possessed the same form as in the fin whale (Fig. 9) the ear plug of the minke whale was found to be so small that unless it was removed within about 6 hr of death it had decomposed. Moreover, in the majority of animals the solid keratinous core showed incomplete, convoluted or no growth laminations (Fig. 9). Of 11 ear plugs obtained in good or fair condition, only one was clearly readable. On the basis of 2 laminations added per annum, this 26.1-ft (7.95-m) male was aged at 3 years.

The majority of baleen plates were not readable by eye, and the extensive wear at the tip shown to occur in winter by Jonsgaard (1951) does not make the use of baleen plates for aging seem very profitable.

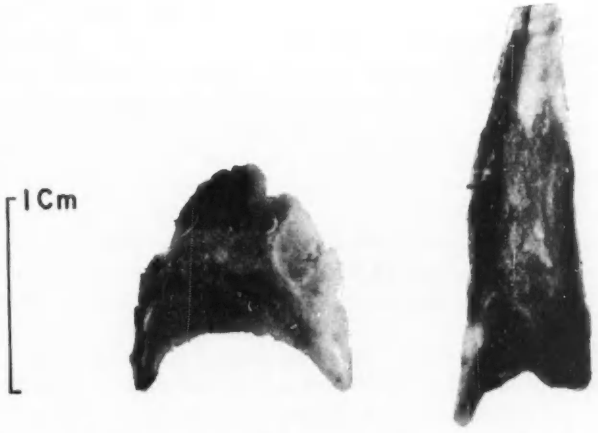

FIG. 9. Sections of ear plugs of two minke whales. Left, of a male 26.1 ft (7.95 m) with 6 laminations; right, of a male length 27.1 ft (8.25 m) which could not be aged.

In none of our adult females were the plates worn at the tip to the extent shown by Jonsgaard in his figure 4 for mature pregnant females taken in April and May. According to his findings, this suggests that our animals had fed for some time after migration into eastern Newfoundland waters, allowing regrowth of the baleen.

Body Scars

Skin scars of unknown origin were found in the majority of animals, their form being shown in Fig. 3. They were found most thickly on the belly but when numerous extended on to the sides and back. They were found in males and females with about equal frequency and density. Three fresh scars were found in one animal; they were 1½ inches (4 cm) in diameter and described in field notes as suggestive of lamprey attack. The healed scar is closely similar to the final stage of healing of a lamprey scar as figured by Pike (1951, fig. 5).

DISTRIBUTION OF MINKE WHALES IN THE NORTHWEST ATLANTIC

The distribution was summarized by G. M. Allen (1916) as follows: "On the western side (of the North Atlantic) it has been recorded as far south as New York and New Jersey, but is apparently rare below the latitude of Long Island. In the Gulf of St. Lawrence and along the east coast of Labrador it is common but in Davis Strait it is rare and only a few seem to reach Baffin's Bay."

Moore (1953) and Moore and Palmer (1955) discovered 4 occurrences of minke whales on the coast of Florida, 3 from the Florida Keys at 24½ to 25°N, and one from the Gulf of Mexico at 30°N. Two of the animals were stranded at known dates, December 28 and mid February, and these animals were both large ones, 27 ft in length or greater.

The most northerly records known to the writer are an immature captured at Sugluk, Quebec, in southwestern Hudson Strait in September 1942, identified from a photograph which clearly shows the white flipper; a sight record by Dr I. A. McLaren off Cape Hope's Advance, northwest Ungava Bay on July 25, 1951; and two probable sight records by Dr M. J. Dunbar in Ungava Bay on August 20, 1954. Mr D. B. Pruden of the Canada Department of Northern Affairs and National Resources identified a minke whale in the estuary of the George River, Ungava Bay on September 15, 1962. Evidently the species regularly summers in Ungava Bay.

Local pockets of minke whales are known to occur in summer in the estuary of the Saguenay River, as reported by Howell (1934) and subsequently by many observers and together with other larger rorquals in the entrance to Passamaquoddy Bay, New Brunswick, by Dr H. D. Fisher (personal communication). Rather frequent reports also from inner Hamilton Inlet and the Narrows at Rigolet, Labrador by Allen (1916) and subsequent observers suggest that such areas of cold, turbulent water have an attraction for minke whales.

The northward movement of minke whales along the east coast of Newfoundland in early summer is shown by the seasonal catches, the maximum influx being in June and July. Evidently the return movement does not occur

before bad weather and short days close down catching in October or November. However a most interesting set of observations was recently given to the writer verbally by Mr Max Tiller of the Newfoundland Department of Welfare, Division of Northern Labrador Affairs, stationed at Nain, Labrador.

He states that minke whales are found off Nain shortly after break-up of the ice in June or July until freeze-up in November or December, being most numerous just before freeze-up. In December 1961 one was trapped in an inlet behind nets set for harp seals (*Pagophilus groenlandicus* (Erxleben)) by its refusal to pass through the immediate vicinity of the nets again. It remained until 4 inches of ice had formed, in spite of repeated rifle-shooting and injury to its snout from breaking ice. A 27-ft female was shot in the same month, and found to contain a foetus 6 ft (2 m) in length. The food at Nain is believed to be mostly capelin, which are taken by harp seals not only during their northward migration in early summer but also in late fall just before freeze-up as they pass the coast southward.

Observations of one or two minke whales in Port au Port Bay, western Newfoundland, in November 1957 and December 1958 can be associated with the schooling of herring which takes place there at that time.

Comparison of our length frequency with those of Jonsgaard (1951), Stephenson (1951) and Omura and Sakiura (1956) suggests that the catches off eastern Newfoundland consist largely of mature animals, with immatures and calves under-represented. Again from the work of these investigators it may be expected that the bulk of these younger animals in summer would occur somewhat to the southward in warmer water. Of this there is some evidence. Allen (1916) listed 26 records of stranded or captured small whales, nine certainly and the rest probably minke whales, from New England waters, principally from the Gulf of Maine between Provincetown, Mass., and Quoddy Head, Maine. Twenty-five of these animals measured 17 ft (5.2 m) in length or smaller, one only reaching 22.7 ft (7.6 m). The dates of 19 of these records ranged from May through October. Dr H. D. Fisher measured one minke whale from the Bay of Fundy, an immature female 18.4 ft (5.6 m) in length caught in a herring weir at Back Bay, New Brunswick on August 4, 1953. Schwartz (1962) records an immature female 16.2 ft (4.9 m) in length from as far south as Chesapeake Bay in July 1959 and likewise infers a southerly distribution of immatures from his and Allen's records.

A new whaling enterprise began in Nova Scotia in 1962, taking minke whales as well as bottlenose (*Hyperoodon*) and pilot whales (*Globicephala*) off the east coast of that province. Future statistical information from this fishery will add to knowledge of the species' local biology.

The extent of the minke whales' distribution offshore is not known but a few observations show them to be present on the offshore Banks; thus, the writer sighted four small, solitary rorquals, presumably minke whales, on a cruise of M/V *Investigator II* in July–August 1957. Two separate individuals were seen near 47°30′N, 50°00′W (about 100 miles east of Cape Bonavista, on the northern edge of the Grand Bank) on August 2, and two at 54°50′N, 53°39′W and 54°15′N,

54°45′W, on the outer part of Hamilton Inlet Bank on August 8 and 9, about 120 and 80 miles, respectively, from the Labrador coast. First mate C. Pardy of the C. G. S. *A. T. Cameron* who had previously hunted minke whales identified them among fin whales on the southern edge of the Grand Bank at 43°08′–10′N, 49°38′–47′W on June 5, 1959.

ACKNOWLEDGMENTS

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A Redescription of the Rare Cottid Fish, *Artedius meanyi*, New to the Fauna of British Columbia[1]

By Richard H. Rosenblatt[2]

Institute of Fisheries, University of British Columbia
Vancouver 8, B.C.

AND

Donald Wilkie

Vancouver Public Aquarium
Box 8, Stanley Park, Vancouver 5, B.C.

ABSTRACT

Nine specimens of *Artedius meanyi* (= *Ruscarius meanyi*), previously known only from the types, have been taken in Howe Sound and the Strait of Juan de Fuca. The genus *Ruscarius*, of which *meanyi* is the type, though retained as a subgenus, is placed in the synonymy of *Artedius*. The subgenus *Ruscariops* Hubbs is considered a junior subjective synonym of the subgenus *Ruscarius* Jordan and Starks. *A. meanyi* is redescribed and compared with the other members of the genus.

INTRODUCTION

Artedius meanyi (= *Ruscarius meanyi*) was described by Jordan and Starks (1894) from two specimens from the vicinity of Point Orchard, Puget Sound, Washington. No other specimens have been recorded and, so far as we have been able to determine, no further specimens had been taken, until the recent captures reported here. Recent collections in British Columbia (made by Wilkie) have yielded nine specimens of *A. meanyi*, all taken in the rocky subtidal.

The capture of these individuals has prompted a re-examination of the status of *A. meanyi*, and of the genus *Ruscarius*, of which it is the type. Our study indicates that *R. meanyi* is properly referable to *Artedius*, but that *Ruscarius* may be retained as a subgenus.

The original description of *A. meanyi* offers little quantitative data. The species is therefore redescribed, on the basis of our material. The format utilized is that of Bolin (1944), so that our description may readily be compared with those given by him. Counts and measurements are shown in Table I.

DESCRIPTION

Artedius meanyi (Jordan and Starks)

Ruscarius meanyi — Jordan and Starks 1894, p. 805, pl. 80 (Type locality, Port Orchard, Puget Sound); Jordan and Evermann 1898, p. 1908 (Copied description

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[2]On leave 1962–1963, Scripps Institution of Oceanography, La Jolla, California.

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TABLE I. Counts, and measurements in millimeters of nine B.C. specimens of *Artedius meanyi*.

	BC 62-495			BC 62-496 BC 62-637		BC 62-901			
Character:	1	2	3			1	2	3	4
Sex:	♀	♂	♀	♀	♂	♂	♂	♀	♀
Standard length	32.8	33.0	22.4	29.9	31.5	34.5	33.9	29.8	28.4
Predorsal	11.2	11.7	8.4	10.8	11.0	12.3	12.2	10.6	10.2
Preanal	17.4	17.7	12.6	15.8	16.5	18.7	18.5	16.5	15.7
Head length	13.5	14.0	9.5	12.1	12.3	14.3	13.7	12.1	11.9
Upper jaw	6.4	6.6	4.6	5.4	6.0	6.6	6.3	5.5	5.3
Snout	3.8	3.9	2.7	3.4	3.3	3.7	3.7	3.6	3.3
Orbit diameter	3.7	3.8	2.8	3.3	3.5	3.9	3.8	3.4	3.3
Body width at pectoral base	6.9	6.6	4.0	6.1	6.0	7.0	6.9	6.7	6.2
Body depth, 2nd dorsal origin to anal origin	5.4	6.0	4.1	5.2	6.2	6.9	6.2	5.1	5.0
Base first dorsal	7.0	8.2	5.1	7.0	7.1	7.7	8.1	7.0	6.8
Longest dorsal spine	4.0	4.5	2.9	3.5	4.1	4.0	4.0	3.2	3.2
Base second dorsal	10.2	10.0	7.6	9.7	9.8	12.2	11.1	9.6	9.2
Longest dorsal soft-ray	5.7	5.5	—	5.0	5.9	5.2	6.0	5.0	5.0
Longest anal ray	3.6	3.8	2.5	3.9	3.5	3.6	3.5	3.5	3.2
Snout to pelvic origin	11.4	11.4	7.8	10.7	11.0	13.0	11.9	11.1	10.5
Longest pectoral ray	10.3	11.0	7.5	9.3	10.0	10.7	10.7	9.1	9.0
Caudal peduncle length	6.9	6.9	4.5	6.0	7.1	7.1	7.3	6.2	5.9
Caudal peduncle depth	2.4	2.2	2.1	2.2	2.4	2.6	2.5	2.0	2.1
Length caudal fin	7.0	6.6	5.4	6.5	6.4	7.5	7.4	6.6	6.9
No. dorsal rays	X–16	X–15	X–16	X–15	X–15	X–15	X–15	X–16	X–16
No. anal rays	12	11	12	12	11	12	11	11	12
No. pectoral rays	15–15	15–15	16–16	15–16	16–16	15	15	16	15L, 16R
No. lateral line scales	36+1	35+1	37+1	36+1	37+1	36+1	35+1	36+1	35+1
No. scale rows	39	36	36	36	40	36	36	36	37
No. scales in longest row	13	12	12	12	12	12	10	11	11

of types); Halkett 1913, p. 99 (Name only); Kincaid 1919, p. 29 (Name only); Hubbs 1928 (Name only); Schultz and de Lacey 1936, p. 127 (Synonymy); Schultz 1936, p. 177 (Name in key).

Body short and chunky, subcircular anteriorly, depth of body at dorsal origin about equal to width at pectoral base. Caudal peduncle slender, its depth 2.2–2.5 in its length and 1.1–1.2 in orbit. Head large and depressed, 2.3–2.5 in standard length. Width of head about 1.5 in its length. Maxillary extending to a vertical from posterior margin of pupil, its length 2.0–2.2 in head. Teeth in jaws small, conical, recurved and pointed. Vomerine and palatine teeth similar in shape to jaw teeth, set in two irregular rows. Profile of head convex from dorsal origin to upper lip, snout about equal to eye. Occipital region slightly concave (flat in smallest individuals). No spines on top of head. Upper preopercular spine bifid (lower fork poorly developed in one individual) curved upward; second spine directed backward, third spine downward, fourth down and forward.

Ctenoid scales present on top head, along lateral margins of interorbital space, snout, suborbital, cheek above the level of the posterior end of the maxillary, and on opercle. (These

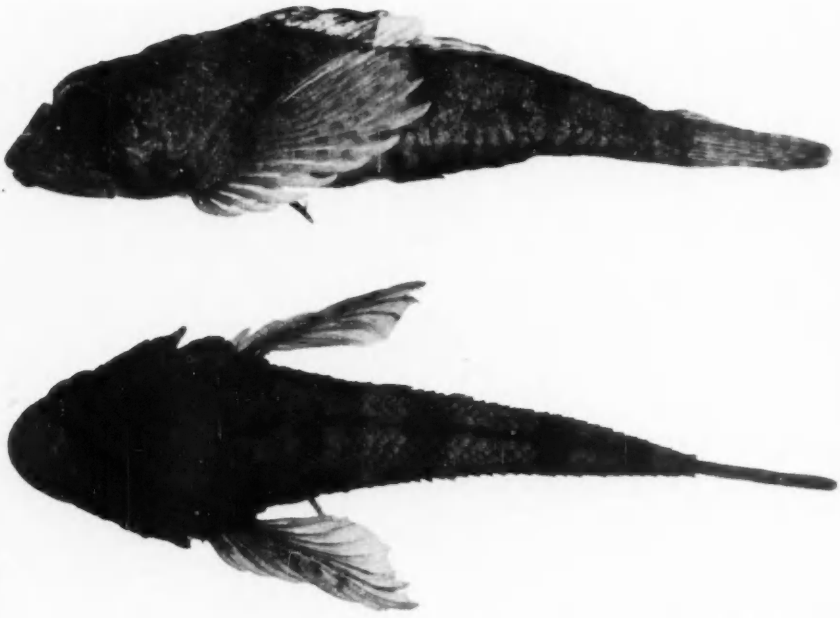

FIG. 1. *Artedius meanyi*. Lateral and top views of a 33.9-mm male from Howe Sound, British Columbia (BC 62–901). (Photos by K. Sandercock.)

scales are larger and more thickly set than those of *A. creaseri*.) Four or five irregular rows of ctenoid scales on upper surface of eye. Dorsal scale band on body continuous anteriorly with scales on head, which are similar in size, extending posteriorly to base of caudal; bands of the two sides closely approximated posteriorly, but no scales on median line of caudal peduncle. A small naked area (¼ to ½ eye diameter) at nape. Dorsal scale band in contact with lateral line back to twelfth to seventeenth lateral line scale, and never separated from it by a gap more than two scales wide. A few small scales behind opercular flap, between lateral line and pectoral base. Lateral line scales about twice as broad as scales on back; with ctenoid margins.

No cirrus on nasal spine. A small slender flap at upper posterior corner of maxillary. A single cirrus on eyeball arising at base of fourth to sixth scale of ventral scale row. Preorbital cirrus long and fingerlike, its length 3.0–3.5 in eye. Postorbital cirrus developed as three (exceptionally four) subequal tentacles which arise from a common base. Length of longest tentacle about 2 in eye. A double row of slender, fingerlike tentacles extending back from each postorbital cirrus, first pair just behind upper posterior corner of orbit, second pair about midway between first pair and end of skull, third pair at rear corner of skull. A pair of tentacles just above upper corner of gill opening. A pair of tentacles at tip of opercular spine. One or two tentacles at base of upper preopercular spine and a small cluster between upper and second preopercular spines. A tentacle on posterior part of suborbital stay and another on cheek below and usually slightly posterior to it. Sometimes a small tentacle on posterior margin of cleithrum behind upper corner of gill opening. Single or double tentacles on six or seven of the first thirty lateral line scales. The arrangement is remarkably constant. The first tentacle is usually on the fourth scale (fifth in two, sixth in one), the second is on the fifth to seventh (tenth in one), the third and fourth are always on the eleventh and twelfth scales, the fifth is usually on the seventeenth, the sixth is usually on the eighteenth, and the last is on the twenty-second to thirtieth scale. Each dorsal spine terminates in a slender filament.

First dorsal rounded, its base about 1.3 in second dorsal base. Dorsals separated by a distance about equal to pupil diameter. Origin of second dorsal over a vertical from first anal ray. Terminal ray completely free from caudal peduncle. Profile of second dorsal almost straight. In males the first two anal rays are stiffened and curved so that they appear noticeably shorter than the remaining rays. In addition, the skin at the base is thickened and folded. The third ray is slightly thickened and curved. In females the first two anal rays are slender, straight and similar to the remainder. Last anal ray attached to caudal peduncle for about ⅓ its length. Pectoral slightly pointed, its longest ray (eighth) extending back to a vertical from fifth or sixth anal ray. Pelvic base midway between tip of snout and sixth or seventh anal ray. Tip of longest pelvic ray just reaches anus when depressed.

Body ground color of alcohol specimen pale. Back crossed by five bars which extend to the midline. First bar passes below first to fourth dorsal spines, second under fourth to tenth dorsal spines (sometimes split by a pale interspace), third under second or third to fifth or sixth dorsal soft ray, fourth under the eleventh to fourteenth soft ray, and the fifth just behind the second dorsal. An additional narrow bar across caudal peduncle. Body bars most intense at lateral line. Below lateral line a series of thin bars extend to ventral side. Some beneath body bars and some in interspaces. These bars merge ventrally on the posterior part of the body, and surround circular pale areas. Top of head with a dusky streak at back of skull, and another across interorbital space. Two bars radiating out and down from eye, one at lower anterior corner of orbit the other under middle of orbit. A dark area posteriorly, just behind orbital rim. Anterior bar beneath eye continued down across upper lip onto tip of chin, where it meets bar from opposite side. Throat dusky. In females and sexually inactive males the first dorsal is dusky between the first and third spines, and the membrane clear posterior to this. Soft dorsal with pigment along rays, membrane clear. Caudal rays streaked with pigment. Anal and pelvics clear in females and sexually inactive males. Pectoral with faint, narrow bars.

In breeding males, the dorsals and the pelvics are dusky. The first two anal rays are clear, but the remaining nine or ten are black. There is no trace of this coloration in the sexually inactive males.

IDENTIFICATION

Artedius meanyi may easily be distinguished from all of the other British Columbia species of the genus by the almost complete squamation above the lateral line, the presence of scales on the cheek and snout, the well developed slender anterior orbital tentacle, and the trifid posterior orbital cirrus. In addition *meanyi* differs in color pattern, chiefly in the presence of thin vertical lines on the lower sides.

Artedius meanyi may most easily be confused with the Californian species *A. creaseri*. The two species are rather similar in general appearance; both have a chunky body, a large head and large, prominent eyes. *A. creaseri* also agrees with *A. meanyi* in that the head is scaly, the squamation on the upper sides is well developed, and in that there are thin vertical lines on the lower sides. The species do, however, differ in several respects. The major differences are summarized in parallel columns below:

meanyi	*creaseri*
Dorsal soft rays 15–16. Anal rays 11–12.	Dorsal soft rays 12–14. Anal rays 10.
Lateral line scales 35 + 1 to 37 + 1 No tentacle on nasal spine.	Lateral line scales 32 + 1 to 35 + 1. A tentacle at base of nasal spine.
Posterior orbital cirrus developed as three tentacles	Posterior orbital cirrus a broad, fringed flap.
Head cirri in the form of finger-like tentacles.	Head cirri flattened.
Six or seven lateral line scales with cirri.	Thirteen–eighteen lateral line scales with cirri.
Dorsal scale band separated from lateral line by one scale row.	A broad naked area posteriorly above lateral line.
Three or four rows of ctenoid scales on eyeball.	Eyeball naked, or with a few tiny imbedded scales.
Upper preopercular spine usually forked.	Upper preopercular spine usually simple.
Last dorsal ray free from caudal peduncle.	Last dorsal ray attached to peduncle for one-half its length.
First two anal rays of male thickened and curved.	Anal rays of male normal.

GENERIC PLACEMENT

Bolin (1944) has reviewed the California species allied to *Artedius lateralis*. Besides the nominate subgenus, he recognized three subgenera, *Astrolytes* Jordan and Starks 1895, *Axyrias* Starks 1896, and *Ruscariops* Hubbs 1926, all of which had been treated as genera by previous authors. Bolin later (1947) gave reasons for this action, and discussed at length the relationships and phylogeny of the species of *Artedius*.

Ruscarius meanyi fits well into Bolin's definition of *Artedius*, and its inclusion in that genus seems justifiable. *A. meanyi* does differ from all other species of *Artedius* in several respects: The squamation of the back is almost complete, there are three or four rows of ctenoid scales on the dorsal surface of the eye, and the posterior orbital cirrus is developed as three tentacles which arise from a common base. However, in all these features except the last, *A. creaseri* (Hubbs) forms a connecting link between *meanyi* and the other species. In *meanyi* there is scarcely any naked area at the nape (one-eighth of an eye diameter or less in width), and the posterior naked area above the lateral line is narrow (not more than one scale row in width). In *creaseri* the dorsal scale band is well-developed. The naked area at the nape varies from one-third to somewhat less than one-fourth of an eye diameter in width, and the scale band is in contact with the lateral line back to the ninth to thirteenth pored scale. Posterior to this point it is increasingly narrow; under the middle of the second dorsal the naked area above the lateral line is usually about one-fifth of an eye diameter in width (one half in one specimen). This condition is intermediate between the extremes represented by *A. meanyi* and such species as *A. harringtoni*, *A. fenestralis* and *A. lateralis* in which the scale band is progressively reduced. Indeed, with the addition of *A. creaseri* this series forms an almost complete continuum.

Although *A. creaseri* does not have conspicuous ctenoid scales on the eye, five of the eight specimens that we have examined have a few (3–6) tiny, imbedded scales on the eyeball. In addition, one individual has a single, well developed ctenoid scale on the upper anterior margin of the eyeball. Although this condition can hardly be termed intermediate, it does suggest that the presence or absence of scales on the eye does not represent a fundamental difference. Bolin (1936) has reported a parallel situation for the cottid genus *Ricuzenius*, in which the species *R. pindae* has small scales on the eyeball, that in the related *B. nudithorax* are represented by papillae. This leaves only the shape of the postorbital cirrus. However, the shape of this appendage varies greatly between the species of *Artedius*. In *creaseri* it is developed as a flap with a fimbriated edge, in *A. lateralis* it is a slender flap or stout tentacle which may be bifid at the tip, and in *A. fenestralis* it is one or two short fingerlike tentacles, or absent altogether.

For these reasons we believe that *Ruscarius meanyi* should be placed in the genus *Artedius*. *Ruscarius* may however be retained as a subgenus. Hubbs (1926) in erecting the genus *Ruscariops* for *R. creaseri*, recognized the affinities of *creaseri* and *meanyi*. Bolin (1944) redefined *Ruscariops* and placed it within *Artedius* as a monotypic subgenus. *A. meanyi* fits Bolin's definition of the

subgenus *Ruscariops* very well. In addition to the characters given by Bolin, both species are differentiated from the other species of *Artedius* by their short, chunky bodies, small size, and by the presence of thin bars on the lower sides, between the main body bars. These accessory bars are best developed in *A. meanyi*, but are present on most specimens of *creaseri*. The differences between the species, involving fin-ray counts, details of squamation and upper preopercular spine shape, are in our opinion much less important than the basic similarities. The genus *Ruscariops* Hubbs (1926) thus becomes a junior subjective synonym of *Ruscarius* Jordan and Starks 1895.

REMARKS

The specimens described here agree with the description and figure given by Jordan and Starks, with the exception of the number of dorsal soft-rays. Jordan and Starks state that there are fourteen dorsal soft-rays in the syntypes, and their figure agrees with this. Dr Warren Freihofer of Stanford University has kindly checked the counts of the syntypes (SU 3127) for us and has determined that the number of dorsal soft-rays is sixteen in both, which is in agreement with our data.

It is difficult to assess the actual rarity of *A. meanyi*. The species is probably an inhabitant of the rocky subtidal, since all of our specimens have come from this zone, and the types were taken with a dredge, a tool commonly used on the rocky bottom. It is apparent however, that if *A. meanyi* is abundant in some special habitat it is in one which we have not yet sampled. Schultz (1936) comments "Common" for *A. meanyi*, but we were unable to locate any specimens in the fish collection at the College of Fisheries, University of Washington.

Halkett (1913) without comment, listed the range of *A. meanyi* as "British Columbia and Puget Sound". However, the species has not been included in the fauna of British Columbia by recent workers (McAllister, 1960; Clemens and Wilby, 1961). Halkett, in his introduction, mentions that he incorporated unpublished records of B. C. fishes received from G. W. Taylor and Francis Kermode. It is likely however, that if Halkett's B. C. record of *A. meanyi* was based on a specimen, the specimen is no longer in existence.

MATERIAL EXAMINED

Institute of Fisheries, University of British Columbia — BC 62-495 (3): Agate Beach, at Sooke, Vancouver Island, British Columbia; depth, 25 ft; temp., 42°F; salinity (surface) 31.4‰; bottom, boulders set in fine sand over solid rock; Oct. 29, 1962. BC 62-496 (1): Whyte Island, Howe Sound, B.C.; depth, 25 ft; temp. 42°F; bottom, rocks, mussel shells and sand over solid rocks; Nov. 8, 1962. BC 62-637 (1): data as in BC 62-496, except date, Dec. 6, 1962. BC 62-901 (4): Garrow Bay, Howe Sound, B.C.; depth 5 ft; temp. 42°F; bottom, rocks over sand; March 2, 1963.

ACKNOWLEDGMENTS

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The Batfish, *Dibranchus atlanticus* Peters, on the Canadian Atlantic Slopes[1]

By E. I. S. Rees

Fisheries Research Board of Canada
Biological Station, St. John's, Nfld.

ABSTRACT

Occurrence of *Dibranchus atlanticus* on the western Atlantic continental slopes north of the Fundian Channel is discussed. Biological and morphometric measurements were made on 15 specimens.

Deep-water otter trawling surveys, extending down to about 400 fathoms (730 m), have been made in recent years on many parts of the Canadian Atlantic continental slopes by the research vessel *A. T. Cameron*. These surveys were primarily intended to assess stocks of redfish, *Sebastes marinus* (Linnaeus) and *S. mentella* Travin, but, incidentally, they have added to our knowledge of several less common species. Among these is the batfish, *Dibranchus atlanticus* Peters (Fig. 1): a small spiny pediculate fish which apparently reaches the northern limit of its distribution at the southern Grand Bank.

The members of the genus *Dibranchus* are mainly inhabitants of the continental slopes in tropical and temperate regions, although Grey (1956) lists 4 species which reach abyssal depths, and *D. atlanticus* has been found as shallow as 22 fathoms (40 m) (Goode and Bean, 1895). *D. atlanticus* normally occurs at depths between 150 and 710 fathoms (274–1300 m) with the majority being taken at 200–450 fathoms (366–823 m) (Goode and Bean, 1895; Roule, 1919; Koefoed, 1927; Schroeder, 1955). On the eastern side of the Atlantic *D. atlanticus* has been taken near the Cape Verde Islands and off the coast of West Africa (Peters, 1875; Vaillant, 1888; Roule, 1919), while on the western side it has occurred in the Caribbean and the Gulf of Mexico as well as at many localities off the United States eastern seaboard (Goode and Bean, 1895; Schroeder, 1955; Edwards *et al.*, 1962). The greatest concentration of records seems to be in the Nantucket–Hudson Canyon area, but this may be due more to the proximity of the Woods Hole Oceanographic Institution and the frequency of deep-water trawling than to greater abundance.

Dibranchus atlanticus seems to occur quite frequently on the continental slopes from Georges Bank southwards (Goode and Bean, 1895; Schroeder, 1955; Edwards *et al.*, 1962), but there are fewer previous records from the slopes north of the Fundian Channel, the area with which this paper is concerned. One was taken near the southern tip of the Grand Bank by the *Michael Sars* 1910 expedition (Koefoed, 1927), another was brought in by a commercial trawler from the

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mouth of the Laurentian Channel (Anon., 1955) and Schroeder (1955) mentions having taken the species below 200 fathoms (366 m) off Browns Bank. To these can now be added 16 specimens taken during *A. T. Cameron* surveys in 1959–1962. The locations and details of these and the earlier records from the Canadian area are shown in Table I and Fig. 2.

TABLE I. Details of *D. atlanticus* caught on the Canadian Atlantic slopes.

Date	Position	Depth	Bottom temp.	Length	Sex	Notes
		fath	°C	*cm*		
June 30, 1910	42°59′N, 51°15′W	(552)	3.5	3.6	...	*Michael Sars* 1910 exped.
Summer 1952 and 1953	Off Browns Bank	200 +	...	...	...	Schroeder (1955)
May 1955	Laurentian Channel near St. Pierre Bank	...	...	14	...	Commercial trawler (Anon., 1955)
Nov. 9, 1959	42°16′N, 65°09′W	210–260	4.8	8.2	M	*A. T. Cameron*
" "	42°31′N, 64°28′W	350–400	4.3	7.5	M	"
" "	" "	"	"	10.2	M	"
Nov. 10, 1959	42°50′N, 62°48′W	100–110	7.9	16	...	"
May 16, 1962	45°11′N, 56°13′W	150	5.5	12.2	M	"
Nov. 3, 1962	44°22′N, 53°22′W	190–290	4.2	11.9	M	"
Nov. 6, 1962	43°12′N, 60°58′W	284–325	4.5	14.1	F	"
" "	" "	"	"	9.9	M	"
" "	" "	"	"	15.3	F	"
" "	" "	"	"	10.9	F	"
" "	" "	"	"	10.8	M	"
" "	" "	"	"	11.7	M	"
" "	" "	"	"	13.0	F	"
Nov. 22, 1962	43°31′N, 59°49′W	235–350	4.4	10.9	F	"
" "	43°30′N, 59°48′W	326–460	4.2	10.9	F	"
Nov. 27, 1962	44°36′N, 57°10′W	165–175	5.1	10.1	M	"

The distribution of *D. atlanticus* in the Canadian Atlantic area is restricted to the edge of the continental shelf and they do not seem to spread very far into the deep channels which cut into the shelf, even though depths and temperatures in the channels are apparently suitable for the adults. The deep channels of the Gulf of St. Lawrence have been investigated extensively but no *D. atlanticus* has yet been found (Steele, 1958). It is also apparent that, whereas *D. atlanticus* may be encountered fairly frequently in the Nova Scotian area, it can be regarded as rare on the southwest slope of the Grand Bank, at least at depths less than 400 fathoms (732 m); 12 specimens were gathered from 29 drags made at depths between 200 and 400 fathoms (366–732 m) in the Nova Scotian area, but only 1 specimen has been obtained from 59 drags made at these depths on the southwest slope of the Grand Bank by the *A. T. Cameron* and the *Investigator II* during the last 10 years.

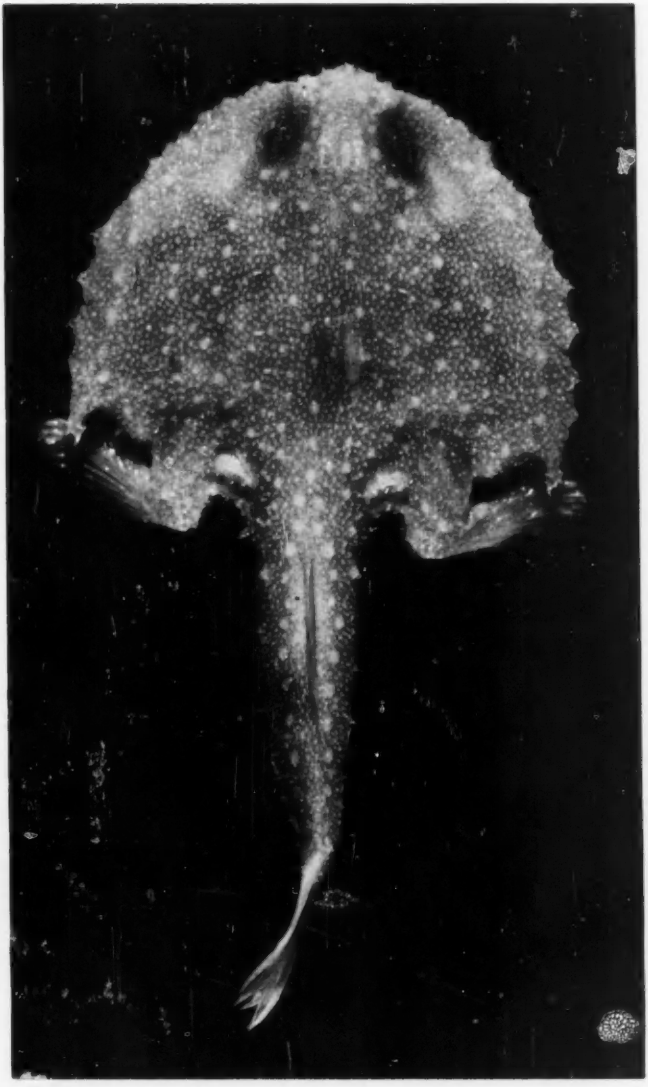

FIG. 1. *Dibranchus atlanticus*, 12.2 cm male, caught at St. Pierre Bank, May 16, 1962.

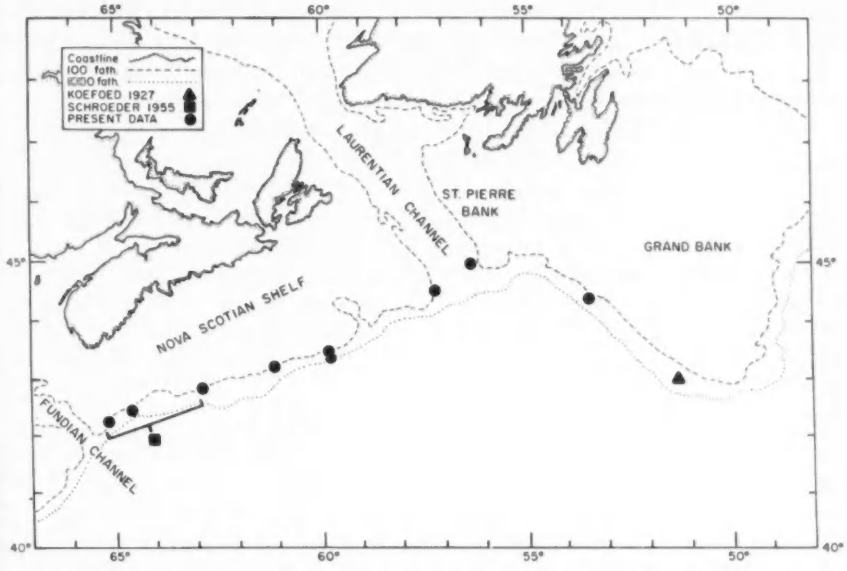

FIG. 2. Locations at which *Dibranchus* has been taken on the Canadian Atlantic continental slopes.

The bottom temperatures, at the positions where most of the specimens were taken in the Canadian area, were mainly between 4 and 6° C, but extremes of 3.5 and 7.9° C are recorded. Elsewhere the temperatures have ranged up to about 20° C at Barbados and to 11.5° C off West Africa (Koefoed, 1927). Assuming that all the specimens are of a single species, this is quite a wide temperature range for a deep-water marine species.

It seems likely, from their structure, that the adults of this species are fairly sedentary, and, since they seem to have a wide temperature tolerance, one must look to the drift, survival and settlement of the eggs and larvae for clues to the factors which determine distribution. *Dibranchus* has a flattened and rolled ovary with the eggs contained in lobules. This is similar to other pediculate fish, including the common angler, *Lophius americanus* Valenciennes, so it is probable that the eggs are laid in a drifting veil. Since *D. atlanticus* belongs to a group with mainly tropical and warm temperate distributions, it is likely that the egg veils require fairly high temperatures for their development. The surface temperature pattern fits in with this thesis; all the records north of the Fundian Channel are from areas where the summer surface temperatures are in the 15–18° C range. These high temperatures are characteristic of the slope water which circulates in the Grand Bank–Nova Scotian sector. The slope water is derived largely from the northern border of the Gulf Stream and has temperatures between 5 and 20° C, though usually it is around 8–12° C at moderate depths (Hachey, 1961). These are temperatures which should suit the larval

development of a warm water species. So the most likely explanation of the distribution pattern of *D. atlanticus* in the Canadian area lies in a need for high temperatures for larval development, coupled with a possible transport of egg veils and larvae from further south by the slope water circulation.

Notes on the colours of the specimens when fresh were made by Mr E. J. Sandeman and the writer. Dorsally they were of various shades of grey-brown with a pinkish tinge and ventrally the colours were similar, though somewhat lighter. The fins were more variable and ranged from white to a brilliant rose red, and the eyes also seemed to vary, from black to blue and green. However, the eye colour was partially due to a Tindal effect and varied with the direction of the light. These colours are similar to those described by Roule (1919), but in our specimens the black peritoneum did not show such a marked bluish cast on the underside of the disc until after the specimens had been preserved in formalin.

Koefoed (1927) noted that there are quite wide variations in the shape of the disc in the specimens illustrated by Peters (1875), Goode and Bean (1895) and himself. He ascribed this to mobility in the opercular bone structure. A similar variation was noted among the Canadian specimens, although most of them had died in the expanded position. This expansion of the disc so that the sub-opercular spines stick out further is probably a defense mechanism similar to that used by the sculpins (Cottidae), and it is natural that they should assume this position when captured and fixed in formalin. The specimens illustrated by Goode and Bean (1895) and Roule (1919) are in the defensive position, but those shown by Peters (1875) and Koefoed (1927) are not fully expanded. In the normal relaxed position the hindmost sub-opercular spine is held close in to the base of the pectoral fin, pointing slightly in towards the tail, and the body becomes thicker and less angular. The body proportions change so that the greatest width of the disc equals about 40% of the total length when the opercular bones are contracted, but in the expanded position it equals 52–56% of the total length.

Dibranchus resembles the angler, *Lophius*, in the possession of enlarged branchial chambers opening by small posterior pores, and it is possible that the mobility of the opercular bones is also connected to the sedentary feeding habits. Willem (1950a) suggests that this type of branchial apparatus allows the fish to lie almost motionless with its mouth open, waiting for prey, while the gills are still kept irrigated without the need for gulping. He also considers that *Lophius* uses a rapid indraught of water into the enlarged branchial cavity to assist in the capture of prey, but he notes (Willem, 1950b) that the inspiration muscles are far less well developed in *Dibranchus* than in *Lophius*.

The stomachs and intestines of 15 individuals from Nova Scotia, St. Pierre Bank and the southwest edge of the Grand Bank were examined. Eight stomachs were empty, but since the contents of the rectum and intestine could be recognised in all cases the information on feeding is based on entire gut contents. Errant polychaetes were the most important food, being found in 11 of the fish (73%). Bottom-living amphipods were found in 2 fish, and bivalve molluscs, ophiuroids

and pycnogonids each occurred once. Two fish contained no food remains at all, and 1 parasitic nematode was found. Crustaceans and molluscs were found by Peters (1875) in the West African-type specimen.

The gonads of the same 15 individuals from the Canadian area were examined, and all were mature (9 male and 6 female). With the exception of a single male caught during May, they were all taken during November and the time of spawning cannot be determined with accuracy. The male taken in May was in spawning condition, having the testis filled with mature tailed sperm, but those taken in November contained mainly spermatocytes, though a few tailed sperm could also be found. The ovaries, which were flattened and rolled up laterally by about 2½ turns, carried the eggs in lobules. Each lobule contained about 25 eggs of varying sizes with the largest eggs in the distal part. The largest eggs in these November-caught fish were 0.23–0.25 mm in diameter in 3 females of length 13.0–15.3 cm, and 0.08–0.15 mm in diameter in 3 females 10.9 cm long. The early stages of maturity reached in November and the condition of the male taken in May are compatible with late spring or summer spawning.

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Temperature, Salinity and Plankton in the Eastern North Atlantic and Coastal Waters of Britain, 1957. III. The Distribution of Zooplankton in Relation to Water Bodies[1]

By B. McK. Bary

Institute of Oceanography
University of British Columbia, Vancouver, B.C.

ABSTRACT

The distributions of 17 species of marine zooplankton from near surface waters are discussed relative to the areas occupied by water bodies (as characterised by surface temperature-salinity diagrams) in the eastern North Atlantic and the coastal waters of Britain. The species' distributions are delimited by the area occupied by the water bodies with which they were associated in the temperature-salinity-plankton diagram, or for some species, by the extended influence of the water pursuant on mixing with another. Oceanic species show distributional features interpreted as indicating movements from north and south towards mixed (transitional) water; species occurring in both oceanic and mixed oceanic-coastal water demonstrate distributional features considered not at variance with movements from the ocean towards the inshore waters. Other, coastal species, are restricted in distribution to water lying shorewards of the position of the shelf-edge. Interspecific variation in relationships to water bodies among species within a group is reflected in more or less limitation of their geographic ranges.

INTRODUCTION

NEAR-SURFACE WATERS of oceanic and coastal areas of the eastern North Atlantic during 1957 have been delineated by temperature-salinity (T-S) diagrams and their geographic distributions discussed (Bary, 1963a). Occurrences and relative abundance of species of zooplankton have been entered on the T-S diagrams (Bary, 1963b). In the resulting temperature-salinity-plankton (T-S-P) diagrams, each of 17 species was found to correlate in a particular way with the water bodies, seasonal fluctuations notwithstanding. The further development of the technique requires that the geographic distributions of the water bodies and of the 17 species be studied together. It is the aim of the present paper to examine this aspect for the surface waters in the oceanic eastern North Atlantic and coastal areas of Britain.

MATERIALS AND METHODS

The nature of the zooplankton collections and hydrographic observations, and the technique and interpretation of the T-S and T-S-P diagrams, have been described previously (Bary, 1963a, b).

In the monthly charts of the present paper (Plates I to XIV), the stations are plotted at which observations of temperature and salinity were made con-

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currently with the towing of the Continuous Plankton Recorder (CPR). Not all stations can be associated with the plankton from one of the alternate sections of silk analysed from the CPR tow, but the number of such stations is small and lack of the data from them affects only details of the overall distributions of species.

The surface water bodies (Plates I to XIV) are reproduced from Bary (1963a). Isolated bodies of high- or low-salinity water distant from a CPR route, and unnecessary to the study of the plankton, have been omitted.

Table I lists the 6 groups of species delineated by Bary (1963b). Each occurrence of each species in the T-S-P diagrams has been symbolised at the corresponding station position in the geographic charts. Thus the relationships

TABLE I. Species of zooplankton included in the study, their groupings and the type of analysis employed in their enumeration (reproduced from Bary, 1963b).

Grouping and species	Animal group	Type of analysis[a]
Warm (southern) group		
Centropages bradyi	Copepod	E
Euchaeta tonsa	Copepod	E
Euchaeta acuta	Copepod	E
Nannocalanus minor	Copepod	E
Warm-transitional group		
Pleuromamma robusta	Copepod	E
Pleuromamma gracilis	Copepod	E
Sagitta serratodentata	Chaetognath	E
Cold (northern)-transitional group		
Pareuchaeta norvegica	Copepod	E
Warm-Transitional-neritic group		
Euchaeta hebes	Copepod	E
Candacia armata	Copepod	E
Centropages typicus	Copepod	T
Spiratella retroversa	Mollusc	E
General-neritic group		
Metridia lucens	Copepod	E
Acartia clausi	Copepod	T
Coastal (neritic) group		
Temora longicornis	Copepod	T
Sagitta elegans	Chaetognath	E
Sagitta setosa	Chaetognath	E

[a]E = relatively large organisms, the numbers of which were estimated by "eye"; T = relatively small organisms, the numbers of which were estimated from a count made during a traverse of the CPR silk with the aid of a microscope.

between species and water bodies, demonstrated in the T-S-P diagrams, are presented with reference to the geographic location of the water bodies.

The data apply only to a depth approximating 10 m.

DISTRIBUTIONS

Warm (Southern) Group: Plates I to III

The species of this group, *Centropages bradyi*, *Euchaeta tonsa*, *E. acuta* and *Nannocalanus minor*, have been recorded from the southern parts of the eastern North Atlantic and are regarded as warm water, oceanic species — Wilson, 1932; Rose, 1933; Colebrook *et al.*, 1961a, b. Neither Ostenfeld (1931), nor Russell (1935a), list them among species collected from inshore areas about Britain.

Almost all occurrences of the warm (southern) species were within the boundaries of the southern water body. The one major exception was in October when specimens were found (Plate III) across the "neck" of a broad, southward intrusion of transitional water. This intrusion was not present in September and had disappeared in November. It was probably a transient feature which may have "entrained" southern water and specimens (warm-transitional specimens were common also — Plate VI).

Specimens were present in the "boundary zones" between southern and transitional water bodies (August, September, November) and between southern water and pockets of very-high-salinity water. During February and August a few occurred just within the very-high-salinity water. Although at times specimens were relatively abundant in southern water in juxtaposition with coastal water (March, July, August), there were no records of them occurring in the coastal water. Occurrences of the species ended abruptly at or near the position where oceanic and coastal waters are believed to have begun to mix, approximately at the position of the shelf-edge (Bary, 1963a).

Sampling was spasmodic in southern areas, but whenever warm (southern) species were collected, their occurrences in the T-S-P diagrams and geographic charts demonstrate the accord which may exist in the distributions of the species and the water body with which they were associated. This would seem to account for these species being recorded in the literature from the warm, oceanic waters in southern areas. It would be of interest to see whether an intensive sampling programme would locate warm (southern) species off western Eire during December to February or March, when southern water is believed to be present there.

Warm-Transitional Group: Plates IV to VI

The species of this group are *Pleuromamma robusta*, *P. gracilis* and *Sagitta serratodentata*. Ostenfeld (1931) records *P. robusta* from southern areas of the North Atlantic and refers to it as an "oceanic temperate" species. Rose (1933) agrees with the southern observations; Farran (1948) records it from eastern oceanic areas. It penetrates the Norwegian Sea (Ostenfeld, 1931; Farran, 1948; Colebrook *et al.*, 1961b), but often only in small numbers (Wiborg, 1955; Hansen, 1960); it also occurs in the North Sea (Rose, 1933; Colebrook *et al.*, 1961b) where it is regarded as an indicator of Atlantic inflow.

Wilson (1932) and Rose (1933) regard *P. gracilis* as being almost as widespread as *P. robusta*, but Farran (1948) states "eastern Atlantic" and "southern and west Ireland". Colebrook *et al.* (1961b) record it most commonly from west and south of Eire, and in low numbers northward towards the latitude of Faroes Islands. It would appear to be a more southern species than *P. robusta*.

Russell (1935b) and Fraser (1952) regard *S. serratodentata* as a warm-water, oceanic species which may penetrate into mixed oceanic-coastal water. Russell uses it to indicate "western water" in the English Channel, but only when that water "was drawn from well towards the Atlantic". Ostenfeld (1931) describes it as temperate and tropical, "distributed in the warmer N. Atlantic west of the British Isles".

In the geographic chart for August (Plate V) the species are present almost exclusively in southern water; from January to March they are predominantly in this water, but also further northwards; at other times, while they were usually more numerous in the south, they were not necessarily in southern water.

Specimens of *P. robusta*, but not the other species, occurred in coastal water (in October). Only rarely (March, October and December) were specimens collected from the "boundary zones" between oceanic and coastal waters.

These data indicate that the species were oceanic, probably originating in southern water, from which they dispersed north into transitional water. The close affinity between the species and oceanic water suggests that records from inshore areas, such as the North Sea, are to be attributed for the most part to shoreward extensions of the appropriate oceanic waters, rather than to the species' presence in mixed oceanic-coastal or coastal waters.

In January, November and December, of the 8 months when routes extended into northern water, *P. robusta* was found beyond, but in close proximity to, the boundary zone between transitional and northern waters. It would seem the species may be able to tolerate northern water for brief periods, but was not resident there. Should transitional water penetrate northwards, as indicated between September and November, *P. robusta*, *P. gracilis* and *S. serratodentata* could probably also move north with it. It would be unlikely, however, that *P. gracilis* and *S. serratodentata* could occur as far northward as the more tolerant and widespread *P. robusta*.

The comparatively widespread oceanic distribution of *P. robusta* and the more restricted distributions of *P. gracilis* and *S. serratodentata* were foreshadowed in the T-S-P diagrams and are apparent in the charts. These distributions agree in general with previous records. However, the present study suggests the species rarely enter oceanic-coastal or coastal waters, and that only *P. robusta* was able to extend into northern water. It would seem that in order to enter these waters the near proximity of transitional water is necessary for *P. robusta*, and probably the actual presence of this water for *P. gracilis* and *S. serratodentata*.

Cold (Northern)-Transitional Group: Plates I to III

Pareuchaeta norvegica was the species of copepod available in the cold-transitional group. It is regarded as an "arctic" species which penetrates southwards into more temperate waters of the eastern North Atlantic. It also

occurs in the deeper Norwegian coastal waters and in the Skagerrak (Sars, 1903; Ostenfeld, 1931; Rose, 1933; Colebrook *et al.*, 1961b). It is usually a deep-living species (Sars, 1903; Ruud, 1929; Ostenfeld, 1931; Rae and Rees, 1947) which seasonally migrates towards the surface (Hansen, 1960).

Although the first few specimens of *P. norvegica* occurred (April) in cool transitional water, they were adjacent to an intruding tongue of northern water and were collected at night (*see* John and Brown, 1958, plate XIII, April; route 134X). In May and June *P. norvegica* was present only in the northern water; it was absent throughout the area in July. During August, September and October it was collected only from transitional water, but sampling did not extend into northern water; in September it occurred towards the south of the area occupied by transitional water. In November it was restricted to northern water and the "boundary zone" between northern and transitional waters. By December it had disappeared from the area. These occurrences of *P. norvegica* were usually not far removed from northern water influences, except for a few specimens in August and when it was common in transitional water in September. It was collected once (October) from mixed oceanic-coastal water.

Pareuchaeta norvegica is a widespread oceanic species. This accords with the broad nature of its relationships to northern and transitional waters in the T-S-P diagrams. Its northern centre of distribution and southward dispersal agrees with the previous records. Seasonal, downward migration probably accounts for its absence during December and early months of 1957; its absence (from northern water) in July may have resulted from avoidance of the unusual conditions at that time, south and east of Iceland (Bary, 1963a).

Warm-Transitional-Neritic Group: Plates VII to IX

The species of this group are *Euchaeta hebes*, *Candacia armata*, *Centropages typicus* and *Spiratella* (*Limacina*) *retroversa*. Vane (1961) regards the distribution of *S. retroversa* as "between and overlapping" that of oceanic and neritic species (i.e. an "intermediate" species — Colebrook *et al.*, 1961a). Ostenfeld (1931) describes it as "boreal Atlantic, oceanic", but states also that it lives in mixed water, avoids pure Arctic water, and occurs in the northern and central North Sea.

Colebrook *et al.* (1961a) also regard *E. hebes*, *C. armata* and *C. typicus* as "intermediate" species, their distributions being similar to that of *S. retroversa*. These species have also been listed or discussed by, among others, Gough (1905), Ostenfeld (1931), Wilson (1932), Russell (1935a; 1939), Farran (1948), and Colebrook *et al.* (1961b). The resulting distributional picture is confused; the species are variously regarded as oceanic, oceanic-neritic, "intermediate" or neritic, but the consensus seems to favour oceanic combined with some ability to occur in neritic conditions.

Both charts and T-S-P diagrams illustrate that the species of the warm-transitional-neritic group occurred with high frequency on both sides of the boundary zones between oceanic and mixed oceanic-coastal waters. This contrasts with the species of the three previous groups.

In February, March, July and August the species occurred, sometimes in relatively high numbers, in the southern water (except *E. hebes*). A few isolated collections of *C. typicus*, *S. retroversa* and *C. armata* were made from transitional water in May, June and August; in September and October, numbers were high and the species were widespread in this water.

At no time were warm-transitional-neritic species collected from northern water, although able to occur in northern latitudes in the presence of transitional water (May and August).

During periods when the species were numerous in southern water, they were abundant in the mixed oceanic-coastal waters of the western approaches to the Channel, but were generally less abundant in the mixed, nearshore waters further northward. During September and October, however, high numbers in transitional water coincided with high numbers in the oceanic-coastal waters of these more northern areas. Periods of abundance in oceanic and oceanic-coastal waters thus were broadly co-ordinated in time and place, a feature shared with the general-neritic group (next section).

These occurrences suggest an oceanic origin for the species, probably in southern water, from which they dispersed into coastal waters.

Euchaeta hebes did not occur in the North Sea, but *C. typicus* and/or *S. retroversa* were present much of the time from January to December. *Candacia armata* occurred near the Skagerrak in February and December and elsewhere in the north of the area during October and November. Most of these occurrences were in or near the inflow originating in the Atlantic, although in July *S. retroversa* extended southward, and in November and December *C. typicus* (and *C. armata* in December) were present eastward of it.

The T-S-P diagrams indicated the species of the warm-transitional-neritic group were less numerous at salinities below about 34.9‰, i.e. in typical coastal water. The fewer specimens collected over the southern of the two routes across the North Sea (remote from the Atlantic inflow) would be in agreement; so would the absence of specimens from the English Channel, even though high numbers might be present at its western end.

The inconsistent interpretations in the literature of the distributions of warm-transitional-neritic species possibly result from their broad relations to the waters of the area and their potentiality for widespread distributions. Within the range of their distributions, fluctuations in numbers in contiguous waters may not always be in phase. Interpretations would depend, in such circumstances, on the breadth of the area covered by a sampling programme, and when and where samples were collected relative to localities in which high and low numbers were present.

General-Neritic Group: Plates X to XII

There are two copepods in this group, *Acartia clausi* and *Metridia lucens*. Their distributions are problematical, in a similar way to the species of the warm-transitional-neritic group. They are very widespread and variously recorded as occurring in all conditions between oceanic and neritic (Gough, 1905; Rae, 1957). Colebrook *et al.* (1961b) discuss a centre of distribution for *Acartia* in

the southern North Sea and another in the eastern oceanic Atlantic; these are regarded as representing separate populations of *A. clausi*.

The relationships of these species to the water bodies in the area are similar in many respects to the warm-transitional-neritic species. There may be some complexity added if populations associated with oceanic and coastal areas are being dealt with simultaneously. However, the southern North Sea *Acartia* may not have been of major concern in samples from the more central areas sampled in the present study. There was insufficient information to designate a separate population of *M. lucens* from the Skagerrak (Rae and Rees, 1947). Data were not available from the Norwegian Sea to compare with Wiborg's (1955) information.

The early occurrences of *M. lucens* in moderately high numbers (February) were in southern and western Channel waters. It then rapidly extended northward into transitional and northern waters (March to May); at the same time it tended to disappear from southern areas. A similar sequence began in southern areas in October and had almost ended in December. *Acartia clausi* increased in May to moderately high numbers in cool (northerly) transitional water, but there were few specimens in inshore waters. Its subsequent rapid increase (June, July) and decline (August to October) was mostly restricted to this water, although when most abundant it spread southwards into warmer transitional water and into oceanic-coastal water.

In the oceanic-coastal waters west of Britain, *A. clausi* was present in approximately similar numbers to, and concurrently with, its occurrences in the open sea. The numbers of *M. lucens*, on the other hand, often were higher in oceanic-coastal than in oceanic water, (chiefly August, perhaps September, October and November). In the oceanic waters during these four months numbers at first increased and then decreased. Nevertheless, superimposed on this situation was the general trend that when *M. lucens* was abundant in oceanic waters it was also abundant in adjacent inshore waters. Conversely, when reduced in numbers in oceanic waters, it became reduced, at least relatively, in the inshore waters (May to July, October to December).

The fluctuating abundances of *M. lucens* and *A. clausi* in the oceanic Atlantic appear to correlate with their occurrences in the northern North Sea. Possibly this was associated with inflowing Atlantic water (Bary, 1963a). In general terms, it seems that *M. lucens* and *A. clausi* entered the northern North Sea (or increased in numbers there) at some time after the species had begun to increase in the oceanic Atlantic, and tended to disappear from the northern North Sea during the early stages of the decrease in the oceanic water. This sort of relationship could be explained if a moderately high level of numbers had to be maintained in the Atlantic (in a location such that specimens would be entrained in the inflowing water) before they could be transported into the North Sea in sufficient numbers to be collected by the CPR. No doubt other factors such as breeding, or a resident population, or seasonal vertical movements in the northern and central North Sea could add further complexity to this view.

The T-S-P diagrams have demonstrated that *M. lucens* and *A. clausi* have broad relationships to the waters in the area surveyed. Therefore, they have the potentiality for the widespread distributions referred to by previous investigators. However, they are probably oceanic species which occurred secondarily in coastal waters (the possible neritic population of *A. clausi* apart). *Metridia lucens* was more plentiful in the warmer than the cooler oceanic waters and probably its centre of distribution was in, or in the vicinity of, southern water; its occurrences in northern water are a complicating factor requiring elucidation. The distribution of *A. clausi* suggests a cool transitional species with some ability to inhabit warmed northern water. The two species moved freely across the boundary zones between some, or all, of the oceanic water bodies and between oceanic and oceanic-coastal waters. In the latter, *M. lucens*, but not *A. clausi*, was present at times in higher numbers than in offshore waters. Numbers in coastal waters west of Britain were affected by the fluctuations in abundance in adjacent oceanic water; and the presence, or absence, of the species in the North Sea appears to have been correlated with periods of high and low abundance in the oceanic Atlantic. Such features require extensive material and a knowledge of the relationships of the species to the waters throughout the area to aid in the interpretation of their distributions.

Coastal (Neritic) Group: Plates XIII and XIV

The distributions of the three species of the coastal (neritic) group have been well documented for the waters about Britain. *Sagitta setosa* is described as having its centre of distribution in the southern North Sea and English Channel (Russell, 1935b); and of being "typical of indigenous North Sea water" (Fraser, 1952). *Sagitta elegans* inhabits principally mixed oceanic-coastal water (Russell, 1939; Marshall, 1948; Fraser, 1952). Furnestin (1938) found that *S. setosa* was associated with salinities usually less than 35‰, and *S. elegans* with salinities usually greater than 35‰. *Temora longicornis* is described by Ostenfeld (1931) as "neritic, boreal and temperate"; he also states "it follows on the whole, the coasts". Other investigators have regarded it as a coastal species which may be carried into oceanic water (Rae and Fraser, 1941; Wiborg, 1955). Colebrook *et al.* (1961b) illustrate concentrations of *T. longicornis* in the southern North Sea and in the southern Norwegian Sea, over deep water. They regard it as neritic in the North Sea, but from its overall occurrences as a "link between intermediate and neritic distributions".

In the geographic charts, *T. longicornis* is seen to occur over much of the North Sea routes; during September and October specimens were also collected north of Ireland and Scotland, from mixed oceanic-coastal waters. In July it was collected near the south coast of Iceland (not shown in the chart for July) from northern water; conditions however, were unusual in the area at the time (Bary, 1963a).

Sagitta elegans was collected from the area of the western Channel, or seawards towards the boundary zone between oceanic-coastal and oceanic

waters. It was present in December in the North Sea[2], associated with the Atlantic inflow, and on one occasion (September) from north of Ireland. Specimens occurred in transitional water, southwest of Eire, in November, but in low numbers compared with adjacent samples within the oceanic-coastal mixture. *Sagitta setosa* occurred in the English Channel (but not in the western Channel) and in the North Sea in November and December. The distributions of *S. elegans* in and westwards of the western Channel, and of *S. setosa* within the Channel, were distinct, which corresponds respectively with "oceanic-coastal" and "coastal" waters in the T-S-P diagrams. The data available from the North Sea are too few to generalise. The distributions of the species in relation to the waters of the coastal areas agree with previous records, even to the occurrence (July) of *Temora longicornis* in water which may have been oceanic.

DISCUSSION

The T-S-P diagrams demonstrate those relationships between species and water bodies which may have been regulating the species' occurrences at the time they were collected. The geographic charts display such relationships another way. If the T-S-P diagrams demonstrate a close affinity between a species and a water body, it will also be shown geographically. The T-S-P procedure entails demonstrating from *field* data that a relationship exists between species and water bodies in an area and then using the relationship to provide an explanation of "why" the species are distributed in particular ways.

Species occurred within the limits of the water body, or of its influence in a mixture. It can be inferred, therefore, that a species collected beyond the area normally occupied by the waters with which it is associated was probably carried there by the body of water in which the appropriate conditions existed. In such circumstances it is not the geographic location of the plankton sample, but the demonstration of the species' relationships to definable limits of the environment, that is important.

Fluctuations in numbers of specimens may lead to a situation in which, although the appropriate water body is present continuously in an area, the species may occur in high numbers at one time, or be rare or absent at another; or a tolerant species which has originated in one water body and entered another may occur in different numbers in the two waters (e.g. *M. lucens*). Here again, it is not the geographic location of samples which is important to interpreting such occurrences, but the relationships of the species to the water bodies in the area, plus in this case knowledge of species' fluctuations.

Northern and southern waters probably moved into the area surveyed in a general west to east direction; at the same time northern and southern waters mixed to form transitional water, the former moving in a south–east or southern direction, and the latter in a north–east or northern direction. Transitional water may have circulated in a clockwise gyre. Northern and southern waters would influence coastal waters either directly, or indirectly via transitional

[2]The Chaetognatha from the North Sea for 1957 were identified subsequently to the routine analysis of collections, and only for November and December.

water. An oceanic-coastal water of mixed properties would be formed which at first gradually, and then perhaps abruptly (at about 35‰?) gave way to typical coastal water.

There were a few species with affinities almost only to southern water, namely, *Centropages bradyi*, *Nannocalanus minor*, *Euchaeta tonsa* and *E. acuta*. Other species extended various distances into transitional water (*Pleuromamma robusta*, *P. gracilis* and *Sagitta serratodentata*); and *P. robusta* (together with *Metridia lucens*), extended into northern water. The fauna of northern water was represented by only *Pareuchaeta norvegica*, which occurred also in transitional water; *Acartia clausi* occurred in cool transitional water and at times in northern water, and it also extended south into warmer transitional water. Other species, regarded as originating in southern areas, probably in southern water, extended into transitional water and also into oceanic-coastal water (*Centropages typicus*, *Candacia armata*, *Euchaeta hebes*, *Spiratella retroversa* and *Metridia lucens*). A group of species was restricted to coastal and oceanic-coastal waters (*Temora longicornis*, *Sagitta setosa* and *S. elegans*). These general distributions conform with the physical features, but there are numerous details which demand investigation and clarification.

The distributions discussed are for a depth of approximately 10 m. At deeper levels species could be moving from inshore waters oceanwards, but such a movement would probably have little direct effect on the present interpretations of the data. On the other hand, species of southern, oceanic origins (*Metridia lucens*, *Pleuromamma robusta*) occurred in northern water at the same time as species of northern (*Pareuchaeta norvegica*) and cool-transitional (*Acartia clausi*) origins occurred towards the south. The situation requires either, or both, a second source for those species which were being recruited into northern water, or that they moved northwards at a level different from that in which northern and cool-transitional species moved south. The southern species concerned (*M. lucens*; *P. robusta*) are tolerant of a wide range of conditions. If they were being carried in water of the northern branch of the current (which appears to contribute to the northern water (Bary, 1963a), they could probably withstand the modification of that water in its progress northward. They could also tolerate the changes in a vertical direction should they migrate upwards into near-surface northern water from deeper levels.

The species with problematical distributions are those with wide ranges of tolerances; they are the species in the oceanic-neritic groups in the present study. For example, the T-S-P diagrams showed that *M. lucens* tolerated a wider range of conditions than *P. robusta* and it could be expected as a result that *M. lucens* would be more widespread than *P. robusta*. Apart from the occurrences of *M. lucens*, but rarely *P. robusta*, in inshore waters, this was well shown in their respective distributions in northern water. *Pleuromamma robusta* was relatively uncommon in northern water where it occurred in the neighbourhood of the boundary zone with transitional water. *Metridia lucens*, on the other hand, was able to penetrate throughout northern water (e.g. November) to the limit of sampling. The relationships shown by T-S-P diagrams and the geographic

occurrences would suggest that when *P. robusta* is recorded from northern areas such as the Norwegian Sea, it would be in the vicinity of, if not actually in, transitional water; *M. lucens* in the same area, however, need not be in direct association with, or even near, transitional water.

Colebrook *et al.* (1961a) state "the different distributions of a number of species of planktonic organisms may be fitted more easily into a continuous series than into separate types of distribution" (and see their text — fig. 4). Their material was collected by the CPR; their series was based on 9-year means (1948–1956) and because they were able to use geographic occurrences of both species and genera, more material was available to them than to the present study. Had it been feasible to use all of their material in the T-S-P diagrams, relationships to water bodies may have approached a comparable continuous series, instead of the groups of species adopted. For example, an approximation to a graded series of relationships could result if species such as *Centropages bradyi*, *Pleuromamma gracilis*, *P. robusta* and *Metridia lucens* were listed according to their tolerances relative to southern water, and possibly the series could be represented geographically as "continuous distribution". On the other hand, the reactions of species at boundary zones cause discontinuities in distribution which may require that grouping of species be retained.

The "neritic", "northern oceanic" and "southern oceanic" species of Colebrook *et al.* (1961a) are comparable with coastal (neritic), cold (northern)-transitional and warm (southern) species of the present study. However, the occurrences of some of their "intermediate" species, *Metridia lucens* and *Euchaeta hebes*, *Candacia armata*, *Spiratella retroversa* and *Centropages typicus*, together with *Acartia clausi* and *Temora longicornis*, are interpreted somewhat differently as a result of the species' relationships to the waters in the area. It is true the occurrences of these species overlap those of the oceanic and coastal species as Colebrook *et al.* (1961a) state, but as well, several (*M. lucens*, *S. retroversa*, *C. typicus*, in particular) can extend, often in high numbers, to the outer limits of sampling in the oceanic water. Such occurrences indicate a more widespread distribution, at least for these commoner species, than "intermediate" encompasses.

Colebrook *et al.* (1961a) did not classify the distribution of *Acartia* because of their belief that discrete populations exist in the oceanic Atlantic and the southern North Sea. From the T-S-P diagrams and charts it appears that the *A. clausi* discussed herein was probably of the oceanic population, inhabiting cooler transitional water, and occurring secondarily in oceanic-coastal water. In the northern and central North Sea, occurrences of *Acartia clausi* may have been supplemented from the southern North Sea population, but the apparent co-ordination in fluctuations between the Atlantic and central North Sea would suggest the main recruitment was from the Atlantic.

The present study shows that *Temora longicornis* is a highly tolerant, neritic species which can occur throughout conditions in coastal and oceanic-coastal waters. Its tolerance might enable it to survive other conditions on the high-

seas (Colebrook *et al.*, 1961b; Wiborg, 1955), but the T-S-P diagrams suggest it would be present there more usually in a mixture of coastal and oceanic waters, than in oceanic water alone.

The sampling procedure with the CPR and the method of analysing collections do not provide sufficiently detailed results to follow the transfer of specimens from oceanic to oceanic-coastal waters along the western seaboard of Britain. Nor could the movements of organisms in the tongues of transitional water extending southwards along the coast of Eire be determined. The latter water movements would seem to be intimately concerned with the occurrences of species of oceanic origin in the western approaches to the Channel.

Information on the distributions of the 17 species included in the present study was accumulating even before the International Council investigations began in the early 20th century. Numerous investigators have contributed to the sum of knowledge concerning the species' biology, and their oceanographic relationships have been of concern (Hjort and Gran, 1900; Russell, 1939; Fraser, 1952). The conventional technique of illustrating the occurrences of the species geographically in charts (as used in such investigations) could have been followed in the present study. From a series of these, the occurrences of a species and periodic changes in its distribution could have been determined and correlated with salinity or temperature or with water movements. Such correlations would have been generalised ones, as Fraser (1952) has pointed out. The additional information of the species' relationships to the water bodies in the area is important in that it has enabled the occurrences and distributions of the species to be reasonably interpreted, in terms consistent with the nature of these relationships, including the species reactions at boundary zones and their fluctuations in abundance within the limits of the water bodies.

SUMMARY

1. The occurrences and distributions of 17 species of zooplankton are illustrated in monthly charts, for 1957, in relation to the areas occupied by the water bodies delineated by Bary (1963a).

2. Those species closely associated with particular conditions in the T-S-P diagrams are those which are restricted in their distributions. Species tolerant of changes in their environment spread further afield but may be still restricted. Thus species which occurred in southern and transitional oceanic waters are shown not to intrude on the whole into areas occupied by northern or coastal waters. Other species with oceanic centres of distribution, which were tolerant of the change resulting on mixing of coastal with oceanic water, were able to intrude into the mixture and in this were largely, but not entirely, restricted to areas where mixing was taking place. Coastal (neritic) species did not (or rarely) occur in oceanic waters, but showed some differentiation by area within coastal waters.

Some general effects of water movements in the area on the distribution of species near the surface, and in depth, are discussed.

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PLATES I TO XIV

Geographic charts showing the monthly occurrences of species in relation to water bodies in oceanic and coastal waters about Britain during 1957.

Plates I to III	Warm (southern) group. Cold-transitional group.
Plates IV to VI	Warm-transitional group.
Plates VII to IX	Warm-transitional-neritic group.
Plates X to XII	General-neritic group.
Plates XIII and XIV	Coastal-neritic group.

WATER BODIES

B — Baltic outflow
C — Northern (Cold)
Co — Coastal
D — Relatively dilute
S — Relatively high salinity
Tr — Transitional
W — Southern (Warm)
VHS — Very high salinity
>35 — High salinity inflow: North Sea

LEGEND TO PLATES

WARM (SOUTHERN) GROUP

Centropages bradyi ..... (E)* — △

Euchaeta tonsa ..... (E) — ⊘

Euchaeta acuta ..... (E) — ⊘

Nannocalanus minor ..... (E) — ▽

WARM - TRANSITIONAL GROUP

Pleuromamma robusta ..... (E) — ◓

Pleuromamma gracilis ..... (E) — ◐

Sagitta serratodentata ..... (E) — ▬

COLD (NORTHERN)-TRANSITIONAL GROUP

Pareuchaeta norvegica ..... (E) — ⊕

WARM - TRANSITIONAL - NERITIC GROUP

Euchaeta hebes ..... (E) — ⊖

Candacia armata ..... (E) — ●

Centropages typicus ..... (T) — ○

Spiratella retroversa ..... (E) — ◆

GENERAL - NERITIC GROUP

Metridia lucens ..... (E) — ⊕

Acartia clausi ..... (T) — ⊗

COASTAL (NERITIC) GROUP

Temora longicornis ..... (T) — x

Sagitta elegans ..... (E) — ◥

Sagitta setosa ..... (E) — ◢

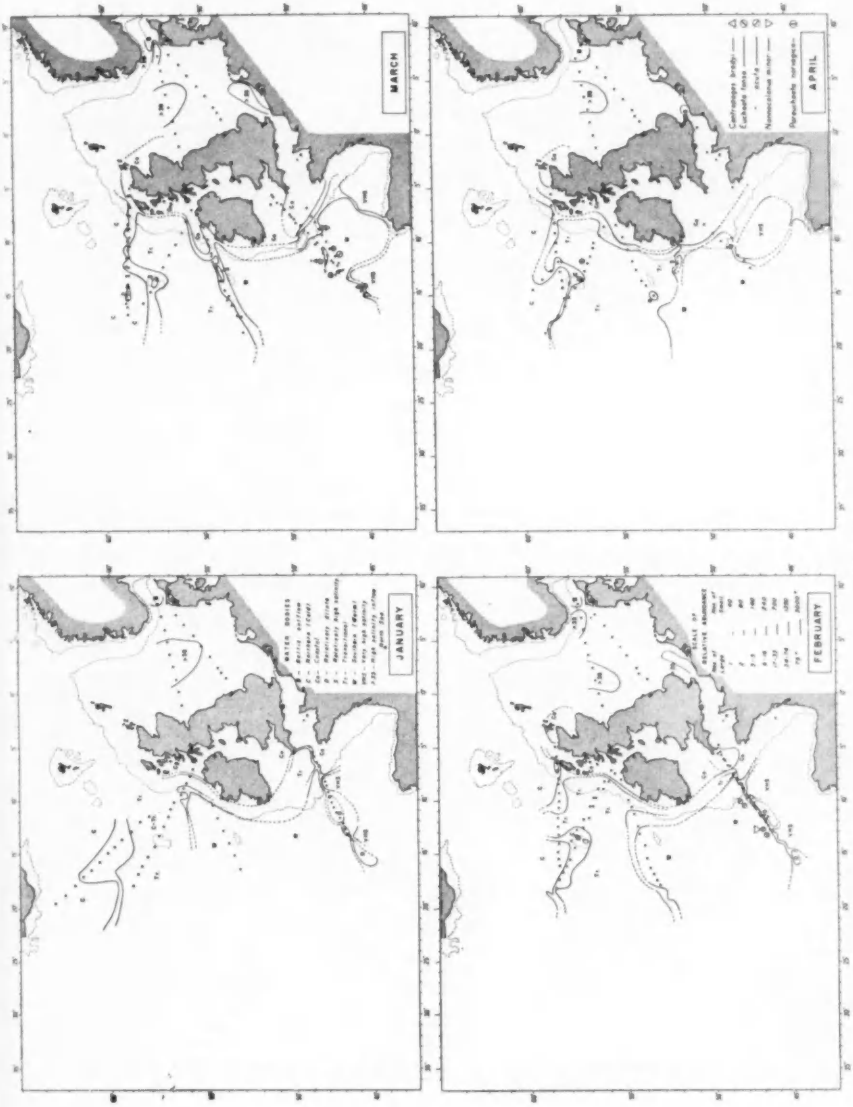
PLANKTON STATIONS IN :

Oceanic waters - - - - - - - - - - - - - - - - - - ●

Coastal waters - - - - - - - - - - - - - - - - - - ○

* E = "Eye - count" = Large organisms

T = "Traverse" = Small organisms



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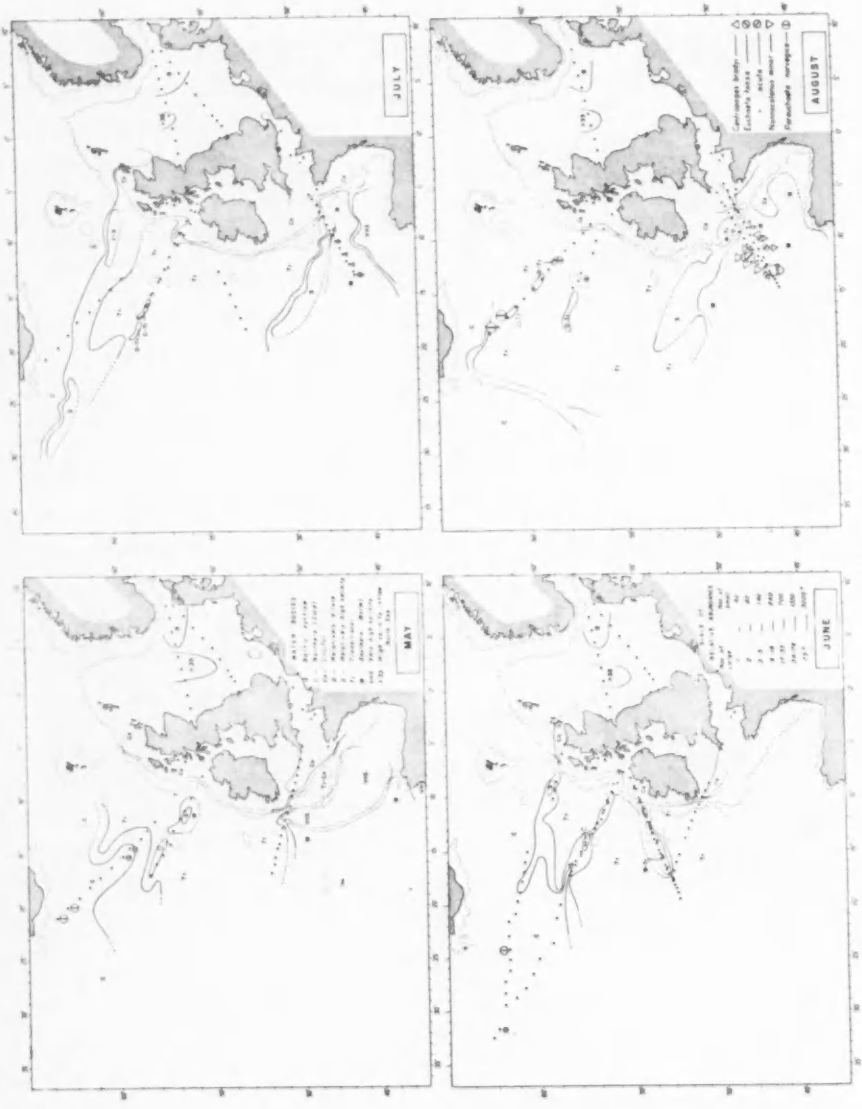

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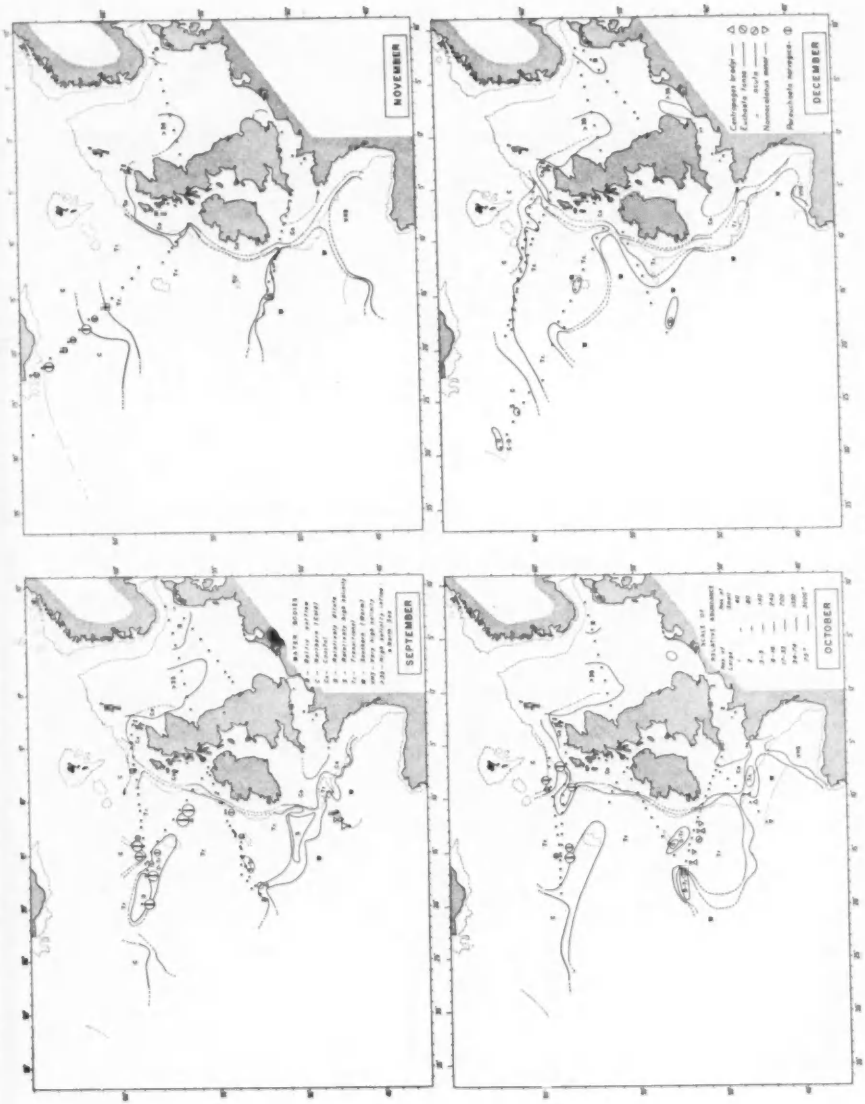

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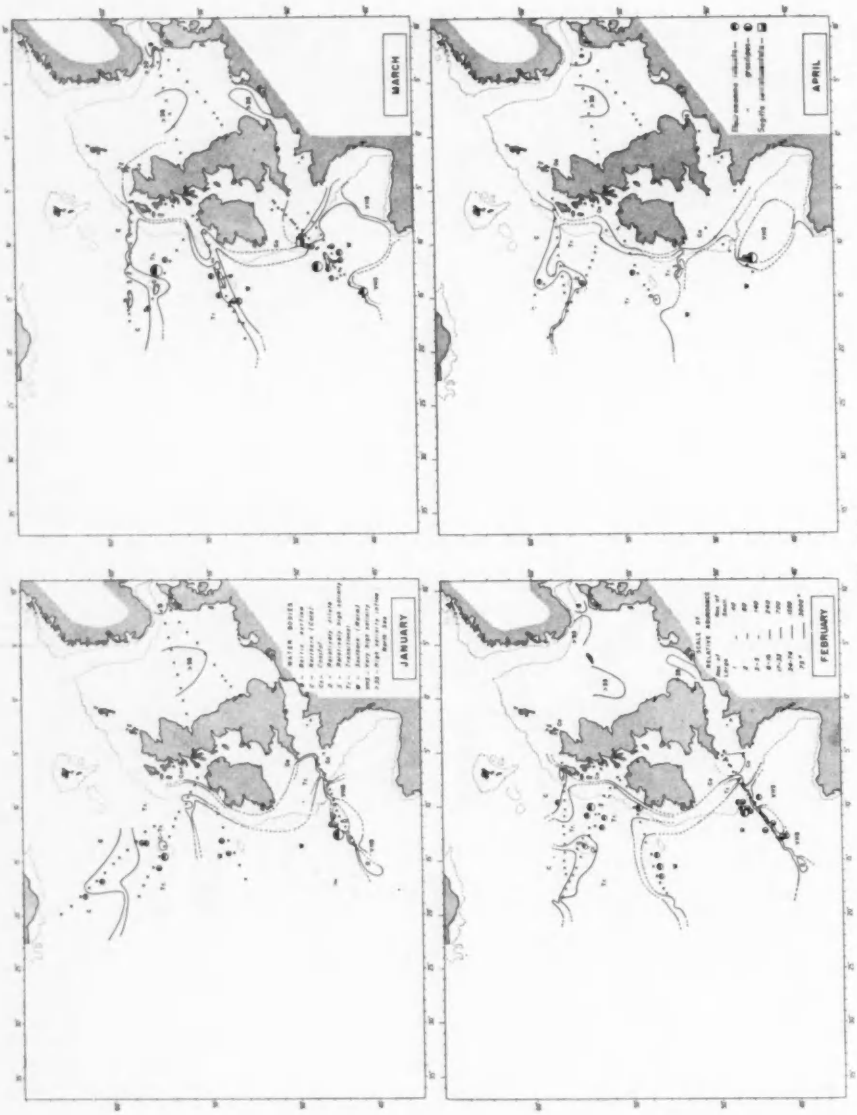

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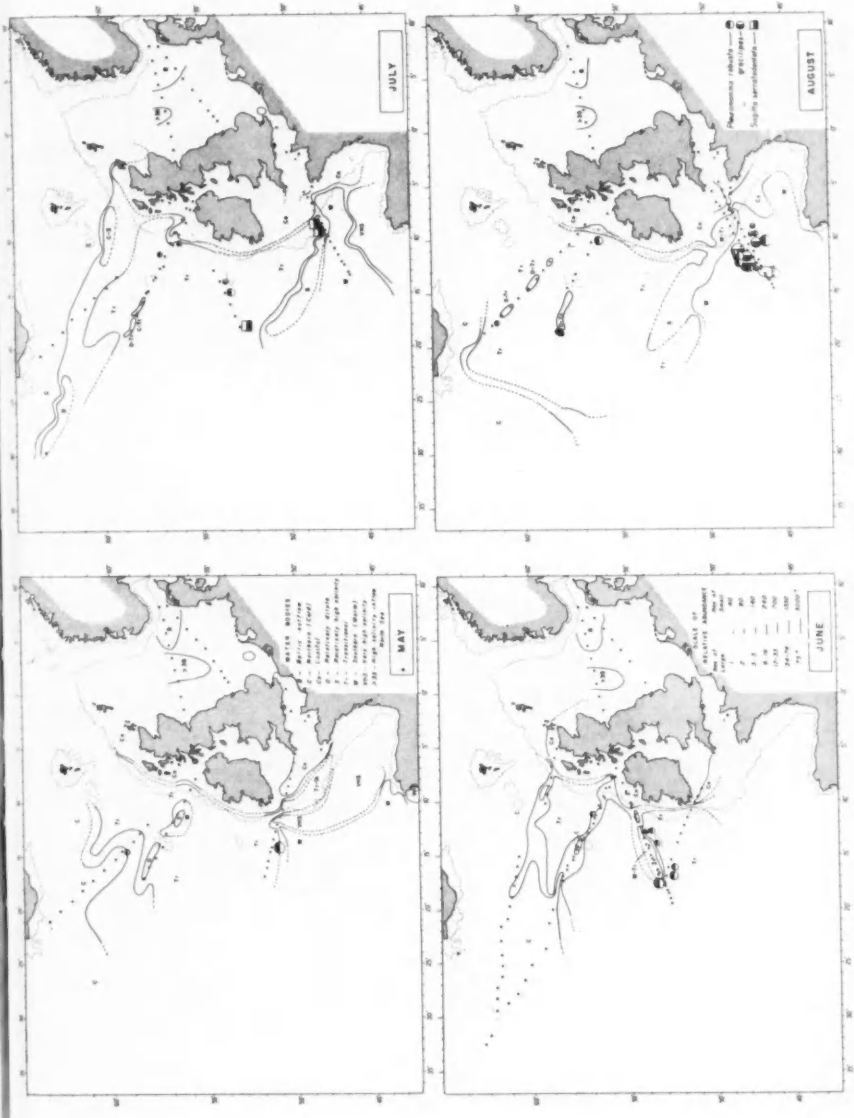

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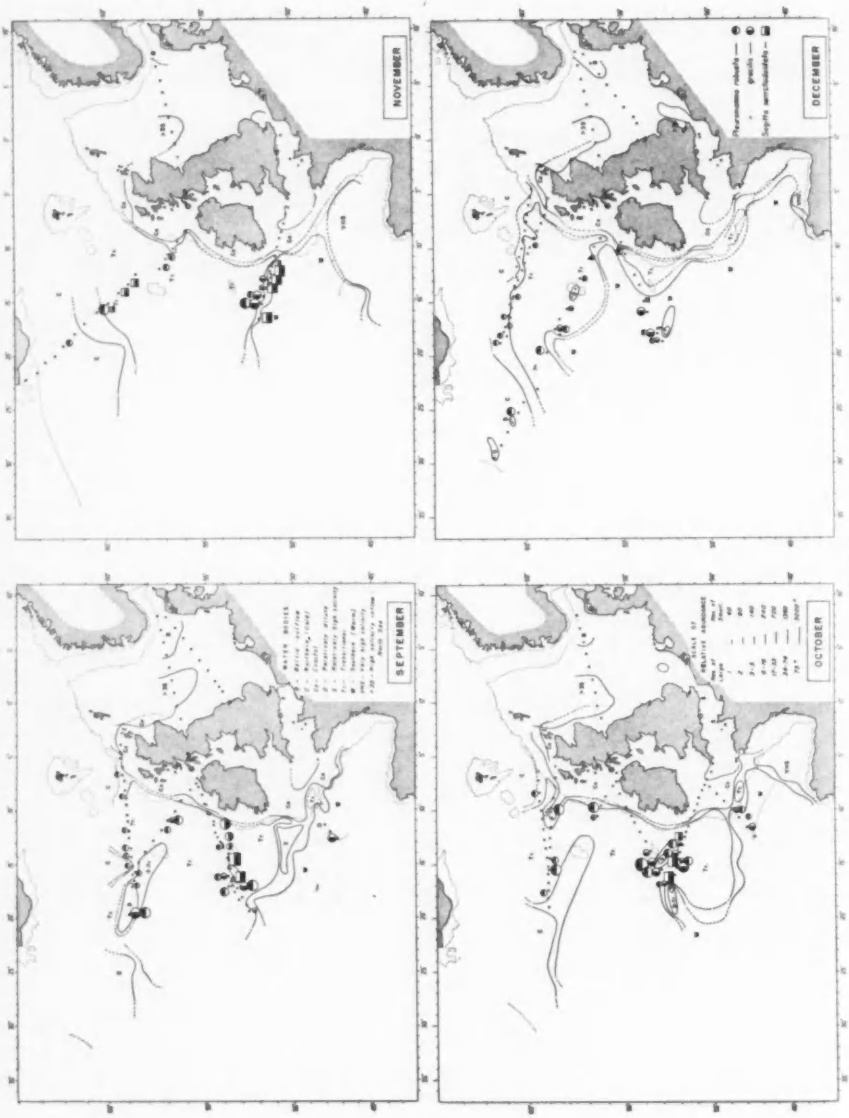

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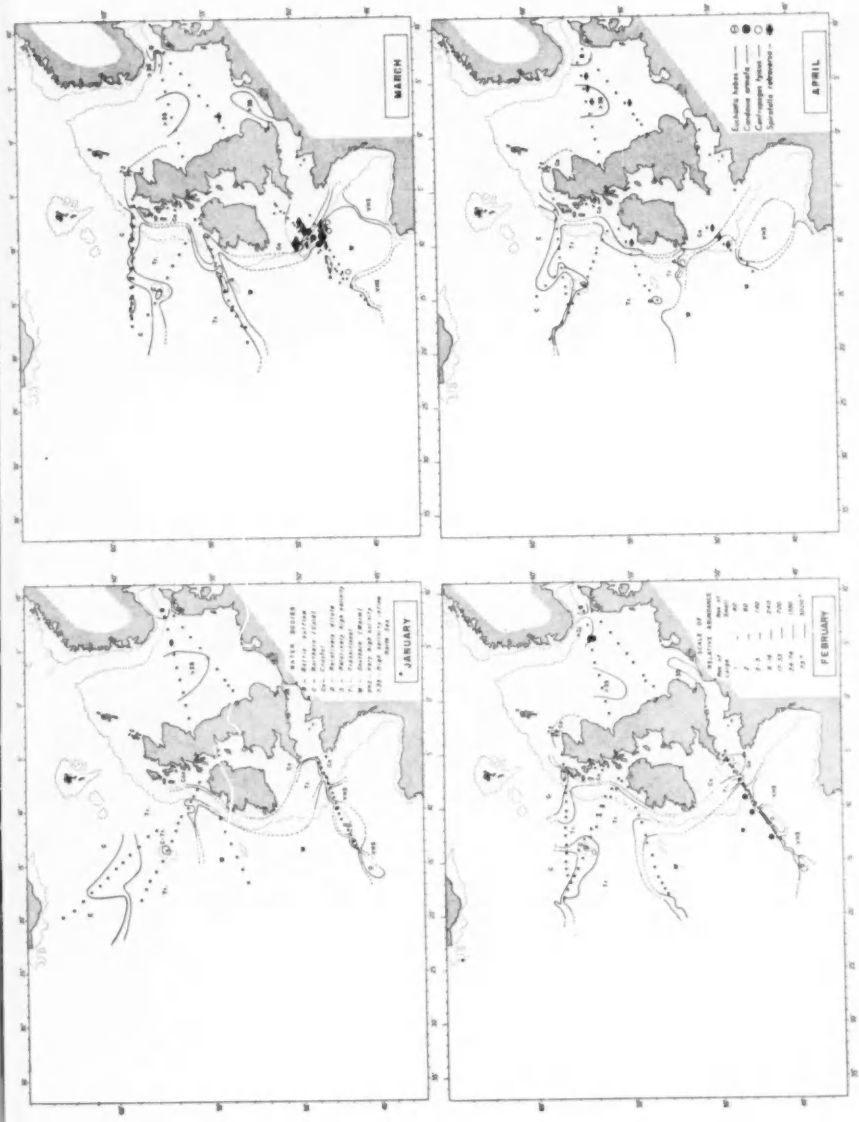


Plate VII.

Plate VI.

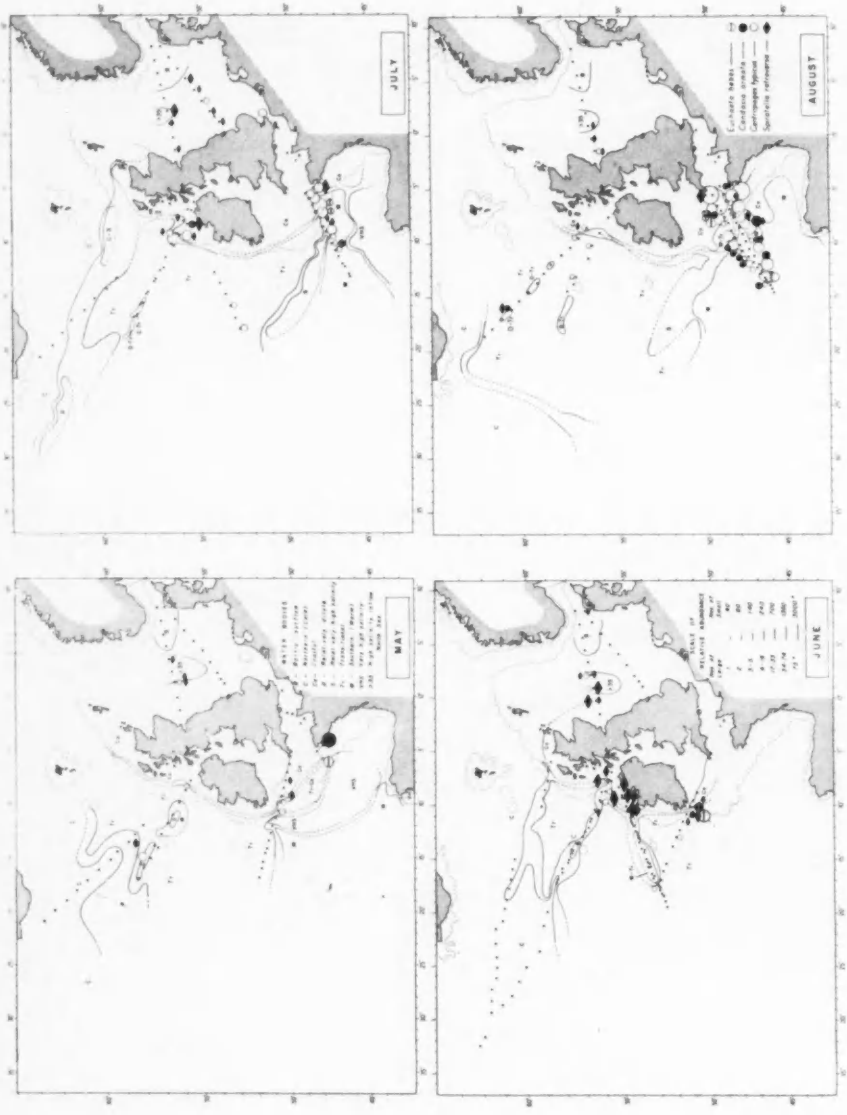


Plate VIII.

Plate IX.

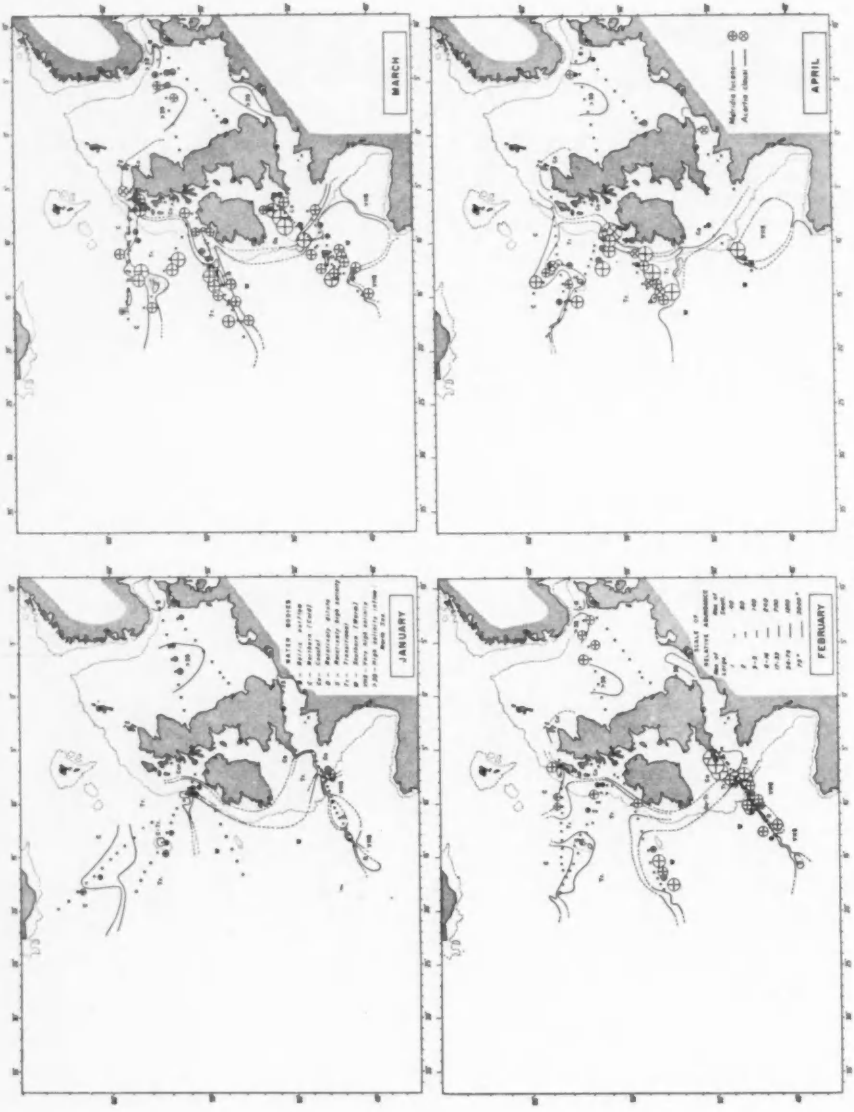
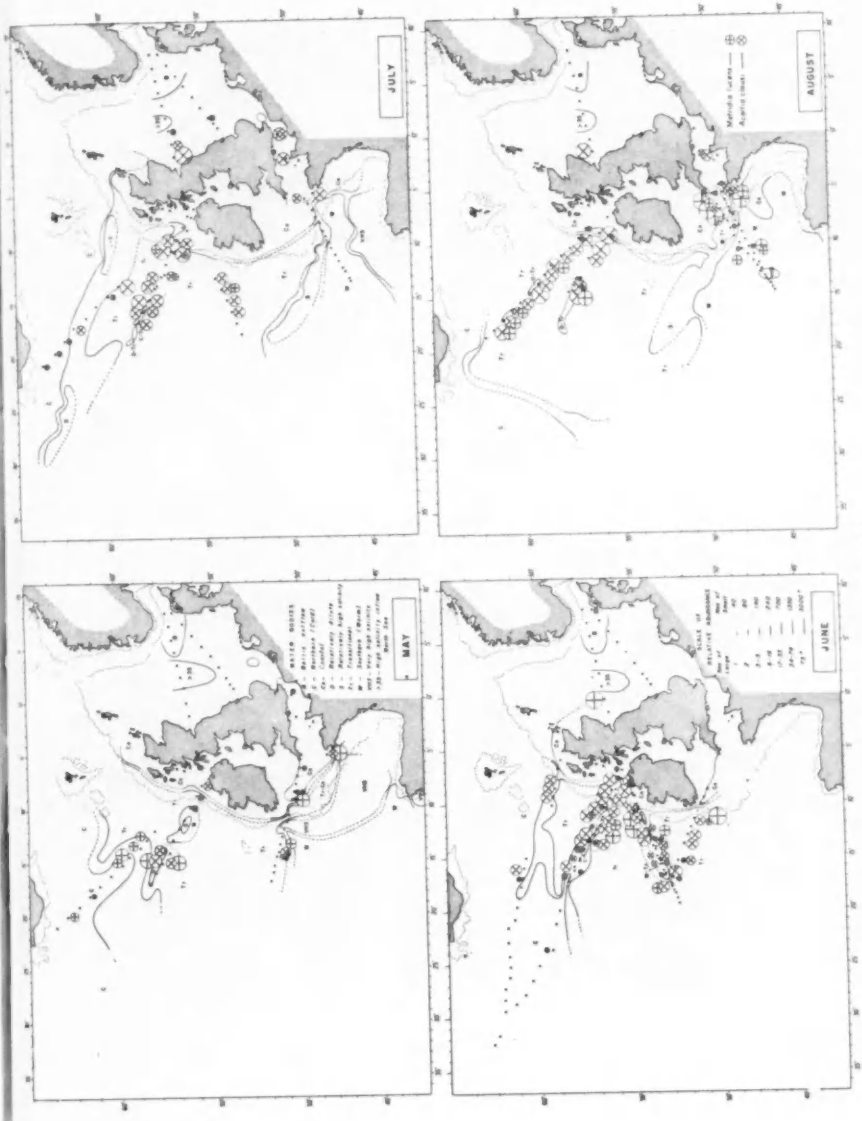


Plate X.



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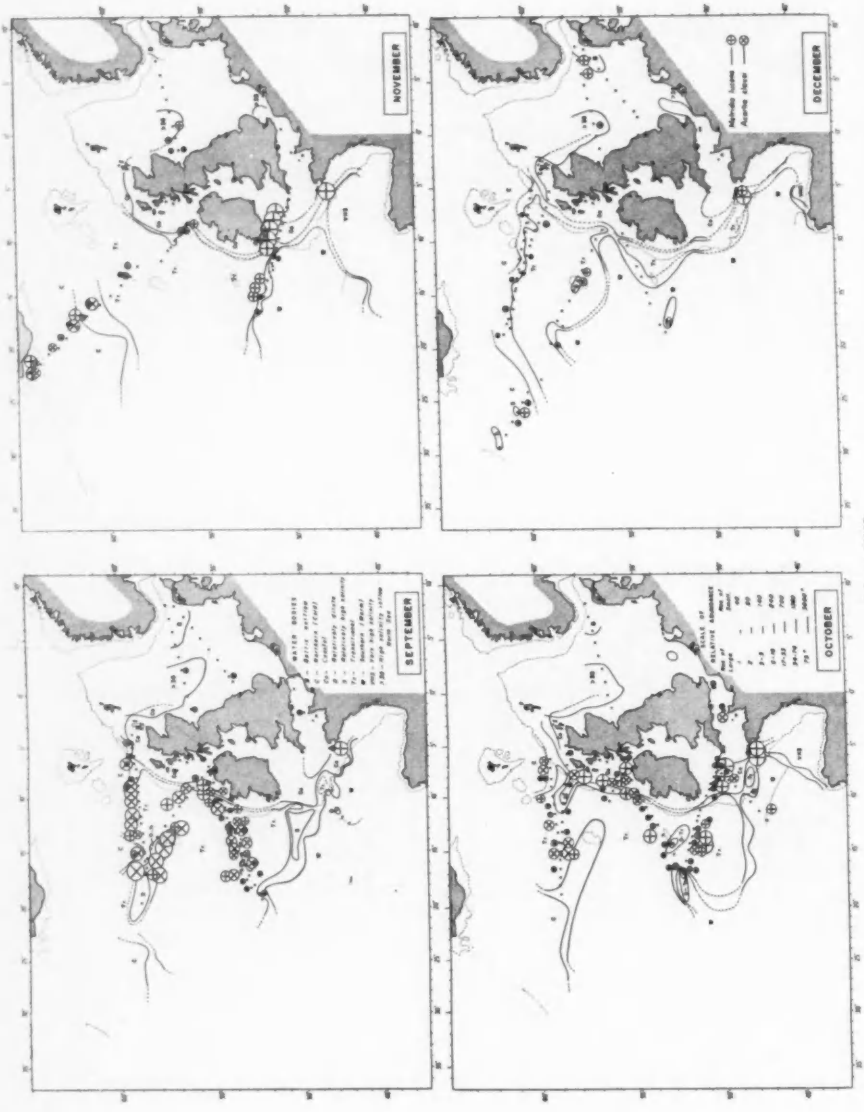

Plate XII.

Plate XIII.

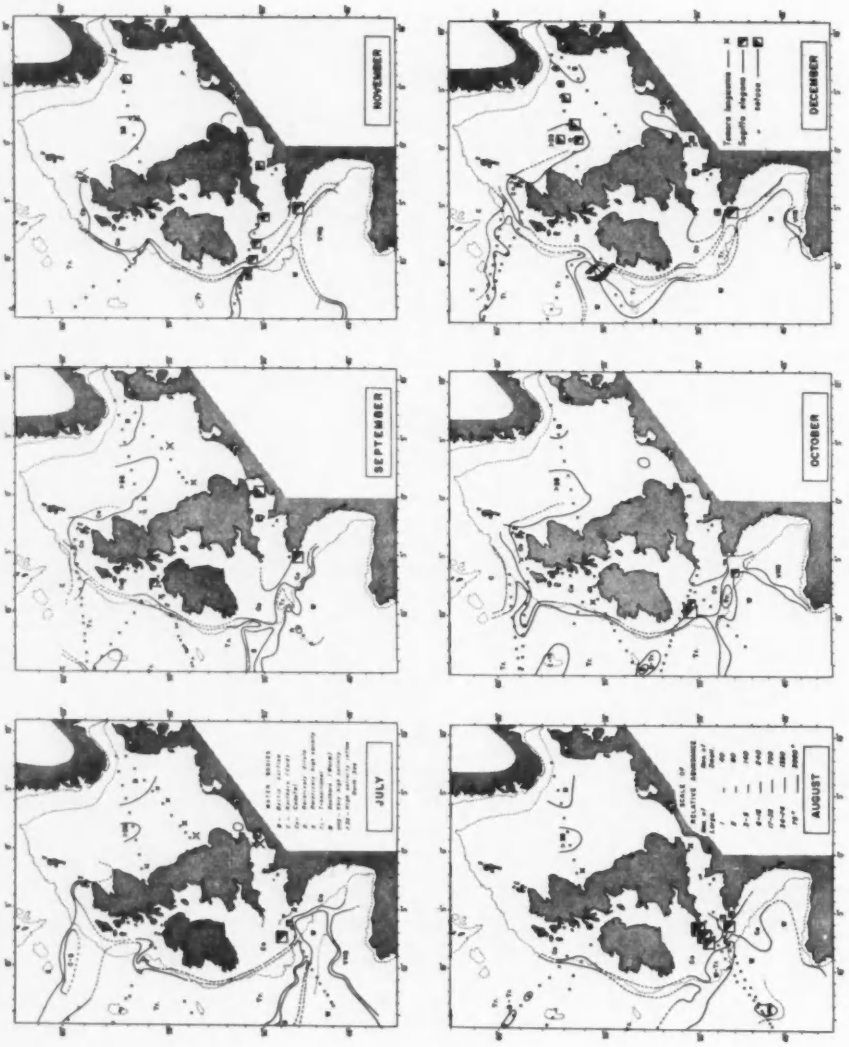

Plate XIV.

NOTES

A Modified Petersen Grab

The deficiencies of the Petersen grab for bottom sampling are well known to anyone who has used it. Yet there have been few significant changes since the first 1913 model.

In benthos sampling at this Station the deficiencies of both the Petersen and the Van Veen samplers were too great to be disregarded. The main problem was that of improper closure due to the rolling and drifting of ships with a variety of relatively large winches unsuited to a slow gradual lift. The solution lay in a more positive closure mechanism.

The principle, suggested by Dr D. B. Quayle of this Station, involved the use of air pressure on a $\frac{1}{5}$ m^2 Petersen grab. A small air cylinder was mounted on the grab and coupled to an air piston which was in turn coupled to the jaws of the grab. Using an appropriate air release valve which is tripped when the grab strikes bottom, the air pressure on the piston closes the jaws. In addition there is a small pressure relief chamber which serves to reduce the back pressure when the air piston is forced down and which also furnishes the air pressure necessary to open the jaws of the grab when air is drained from the upper part of the cylinder.

An ordinary 71 ft^3 (2200 lb) Scuba tank with a "quick connect" coupling is used for charging the small 8- by 3-inch air bottle with a volume of about 1 litre and which operates at a pressure of between 400–500 psi. The grab can be prepared for lowering in less than a minute and between 30 and 40 charges can be obtained from the 71 ft^3 Scuba tank.

Additional modifications were the removal of the sheave and chain from inside the grab to permit a large sample to be taken and the addition of a weight of 50 lb.

The grab thus modified and illustrated in Fig. 1 has operated successfully in a variety of depths and weather conditions.

Messrs K. Sutherland and M. Pope assisted with design suggestions and in construction.

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

J. FLURY

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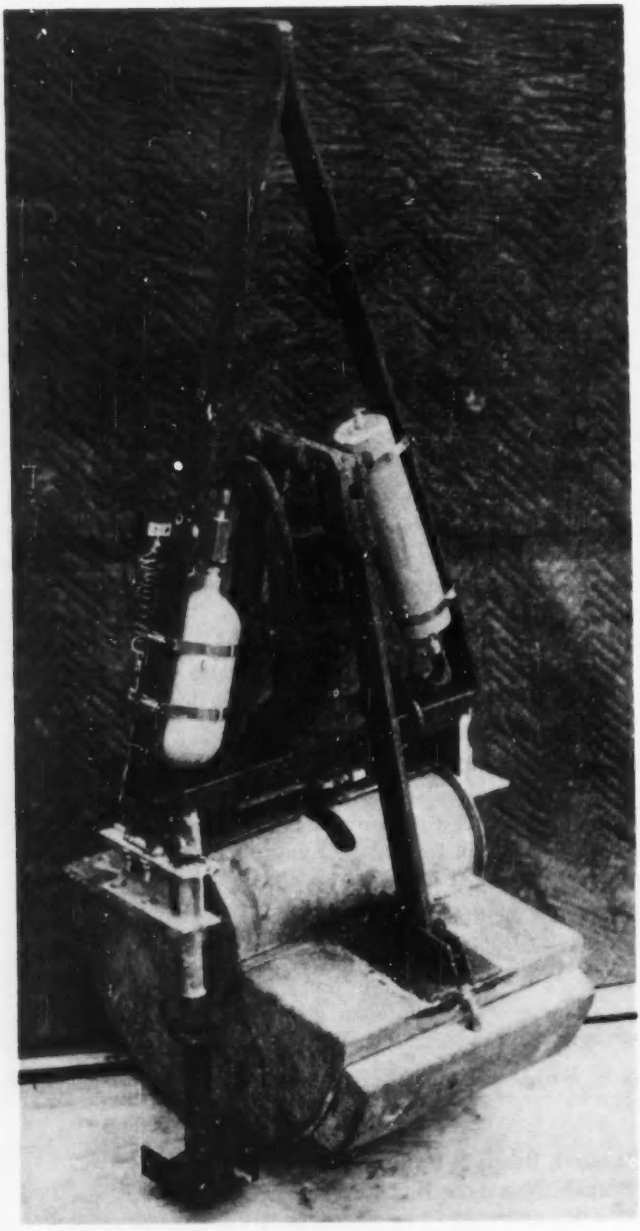

FIG. 1. Petersen grab with air-pressure closing mechanism.

On the Occurrence of 4,7,10,13,16-Docosapentaenoic Acid in Saury (*Cololabis saira*) Oil

It has been reported that the docosapentaenoic acid isolated from saury oil had double bonds in the 4, 7, 10, 13 and 16 positions (Toyama *et al.*, 1959). Although this acid has definitely been isolated from other sources (cf. Ackman, 1963), the isolation from saury oil by the usual procedures implies that this isomer is the principal docosapentaenoic acid, whereas the 7,10,13,16,19 isomer is normally the predominant form in marine lipids (Ackman, 1963).

A sample of saury oil (iodine value 151) courtesy of C. Itoh & Co. Ltd., Central P.O. Box 136, Tokyo, Japan has been analysed by gas–liquid chromatography on a number of polyester substrates with provisional peak identifications by the linear log plot and separation factor procedures (Ackman *et al.*, 1963; Ackman and Burgher, 1963). The results (Table I) indicate that the proportions conform to those normally observed (about 1:10) for the 4,7,10,13,16 and 7,10, 13,16,19 isomers.

TABLE I. Component fatty acids of saury oil.

Fatty acid[a]	Structure	Weight %	Fatty acid	Structure	Weight %
12:0	–	NSA	20:0	–	NSA
14:0	–	9.6	20:1	11[b]	15.6
14:1	?	0.1	20:2	8, 11	NSA
15:0	–	0.2	20:2	11, 14	0.1
15:1	?	NSA	20:3	8, 11, 14	TRA
16:0	–	13.5	20:4	5, 8, 11, 14	0.3
16:1	9[b]	4.9	20:4	8, 11, 14, 17	0.7
16:2	6, 9	NSA	20:5	5, 8, 11, 14, 17	9.2
16:2	9, 12	0.5	21:5	?	0.1
16:3	6, 9, 12	0.1	22:0	–	NSA
16:4	6, 9, 12, 15	0.2	22:1	11[b]	16.5
17:0	–	TRA	22:4	7, 10, 13, 16	NSA
17:1	?	TRA	22:5	4, 7, 10, 13, 16	TRA
18:0	–	1.1	22:5	7, 10, 13, 16, 19	0.8
18:1	9[b]	9.5	22:6	4, 7, 10, 13, 16, 19	9.9
18:2	6, 9	NSA	24:1	?	0.7
18:2	9, 12	1.1			
18:3	6, 9, 12	0.1			
18:3	9, 12, 15	0.7			
18:4	6, 9, 12, 15	4.3			
19:0	–	NSA			
19:1	?	TRA			

[a]Chain length: number of double bonds.
[b]Other isomers may be present.
NSA (no significant amount) = possibly present, but $<< 0.1\%$.
TRA (trace) = present, but $< 0.1\%$.

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The iodine value calculated from the composition given in Table I is 148. The proportions of all major components are similar to those given by Ito and Fukuzumi (1962) for an oil of iodine value 166. In addition to those components listed in Table I there were 0.4% recognizable branched chain fatty acids and about 0.1% each very tentatively identified C_{24} acids with 5 and 6 double bonds.

The saury oil sample analysed, in addition to having a high proportion of myristic acid, has certain unsaturated fatty acids in unusual proportions, also suggesting a predominance of synthesis route (b) over route (a), further rendering it unlikely that the predominant docosapentaenoic acid would be the 4,7,10,13,16 isomer (cf. Mead, 1961).

(a)	(b)
6,9,12-octadecatrienoic	9,12,15-octadecatrienoic
↓	↓
8,11,14-eicosatrienoic	6,9,12,15-octadecatetraenoic
↓	↓
5,8,11,14-eicosatetraenoic	8,11,14,17-eicosatetraenoic
↓	↓
7,10,13,16-docosatetraenoic	5,8,11,14,17-eicosapentaenoic
↓	↓
4,7,10,13,16-docosapentaenoic	7,10,13,16,19-docosapentaenoic

Fisheries Research Board of Canada
Technological Research Laboratory
Halifax, Nova Scotia.

R. G. ACKMAN
P. M. JANGAARD

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Spring Stainless Steel Anchor Tag

For the population study at Heming Lake, Manitoba, an additional fish tag was sought that would provide good anchorage, be easy to apply to fish of all sizes, and not have any protuberances which might tend to catch on nets, brush or other objects, thus increasing the chances of the fish being caught. A tag was designed and used in 1961. It (Fig. 1) consists of a small stainless steel anchor with the identifying disc attached by either stainless steel, tantalum wire or monofilament nylon. The specifications of the anchor were as follows: 0.012-inch, Type 302, spring stainless steel wire; length of anchor $\frac{11}{16}$ inch (17 mm); length of barb $\frac{1}{4}$ inch (6 mm); manufactured by Bohne Industries, Toronto, Ontario, Canada.

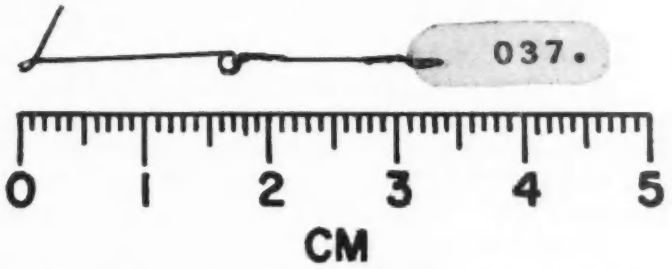

FIG. 1. Stainless steel tag with transparent colourless identification disc.

To apply the tag, a No. 16 syringe needle is inserted diagonally through the fish at an angle below the dorsal fin, between the interneurals and through the skin on the other side. The spring barbed end of the anchor is compressed, inserted in the hollow needle and the needle withdrawn until the anchor is in position between the interneurals. The tagger then grasps the identifying disc and gives it a slight tug which releases the anchor from the needle, causing the spring to open; it should then be firmly anchored between the interneurals. If the tag is properly applied, the small eye of the anchor should be imbedded beneath the scales and only the dangling identifying disc will be exposed.

These tags were applied to the following species of fish in 1961: yellow perch, *Perca flavescens*, 5–10 inches (13–26 cm); common sucker, *Catostomus commersoni*, 6–15 inches (15–39 cm): burbot, *Lota lota*, 13–22 inches (32–57 cm); pike, *Esox lucius*, 8–18 inches (21–47 cm).

A total of 2408 of these tags was applied in 1961, and 426 (18%) were recaptured in the years 1961 and 1962.

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G. H. LAWLER

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